

# The Harttiini (Siluriformes, Loricariidae) from the Guianas: a multi-table approach to assess their diversity, evolution, and distribution\*

by

Raphaël COVAIN\* (1, 2, 3), Sonia FISCH-MULLER (1), Juan I. MONTOYA-BURGOS (2),  
Jan H. MOL (4), Pierre-Yves LE BAIL (5) & Stéphane DRAY (3)

**ABSTRACT.** - The Harttiini are a tribe of Loricariinae poorly characterized morphologically. Within the Guianas (French Guiana, Suriname, and Guyana), six valid species were recognized, including five *Harttia*, and the monotypic *Harttiella crassicauda*. Recent investigations conducted during the last decade by the authors and their co-workers, revealed several unidentified populations of Harttiini. Using a multivariate and multi-table approach unifying morphometry, genetics through DNA barcodes, and ecology-distribution of all populations and species, the global diversity and main evolutionary trends of this group were assessed. The separate analyses highlighted strong structures supporting the validity of three genera: *Harttiella*, *Harttia*, and *Cteniloricaria*, as well as nine new species (six *Harttiella*, two *Harttia*, and one *Cteniloricaria*), and one synonym. The combined analysis established a compromise between the preliminary ones, and revealed their common structure. This structure was found to be linked to the evolutionary history of Harttiini. Their evolution was driven toward adaptations to a definite type of biotope. These included modifications in size and shape, particularly of the caudal peduncle, depending on whether the species colonised rivers or mountainous forest creeks. A longitudinal evolutionary gradient was also highlighted in the geographical distribution of the species despite large overlaps. Notably, *Harttiella* possessed the greatest number of species with the smallest distribution, making each of them highly vulnerable to anthropic perturbations of their environment. Nine new species are described and a key to all species from the Guianas is proposed.

**RÉSUMÉ.** - Les Harttiini (Siluriformes, Loricariidae) des Guyanes : une approche multi-tableaux afin d'évaluer leurs diversité, évolution et distribution.

Les Harttiini représentent une tribu de Loricariinae assez peu différenciée morphologiquement. Dans les Guyanes (Guyane française, Suriname et Guyana), six espèces valides étaient reconnues, incluant cinq *Harttia* et le monotypique *Harttiella crassicauda*. De récentes collectes réalisées lors de la dernière décennie par les auteurs et leurs collègues, ont révélé la présence de plusieurs populations non identifiées de Harttiini. En utilisant une approche multivariée et multi-tableaux unifiant morphométrie, génétique aux travers des codes barres ADN et écologie-distribution de toutes les populations et espèces, la diversité globale et les principales tendances évolutives de ce groupe ont été évaluées. Les analyses séparées ont révélé de fortes structures supportant la validité de trois genres : *Harttiella*, *Harttia* et *Cteniloricaria*, ainsi que neuf nouvelles espèces (six *Harttiella*, deux *Harttia* et une *Cteniloricaria*) et un synonyme. L'analyse combinée établit un compromis entre les analyses préliminaires et révèle leur structure commune. Cette structure s'est avérée liée à l'histoire évolutive des Harttiini. Leur évolution a conduit à des adaptations à un type défini de biotope. Celles-ci incluent des modifications de taille et de forme, en particulier du pédoncule caudal, selon que l'espèce a colonisé les rivières ou les criques forestières de montagne. Un gradient évolutif longitudinal de la distribution géographique des espèces a également été mis en évidence malgré de forts chevauchements. Le genre *Harttiella* possède ainsi le plus grand nombre d'espèces ainsi que la plus petite distribution, rendant chacune d'entre elles particulièrement vulnérable aux perturbations anthropiques de leur environnement. Neuf nouvelles espèces sont décrites et une clé de toutes les espèces des Guyanes est proposée.

Key words. - Morphometry - DNA barcodes - COI gene - Ecology - Multiple co-inertia analysis - New species descriptions.

The Neotropical freshwaters are home to one quarter of the total world ichthyodiversity, with a prediction of around 8,000 extant species out of a mean estimation of 32,000

(Lévêque *et al.*, 2008). In this context, the Guiana Shield region represents one of the most species rich regions of South America, with an estimated 2,200 freshwater fish spe-

\* Supporting files are available online: <http://www.mnhn.fr/sfi/cybium/cybium/numeros/361/sommaire361.html>

(1) Muséum d'histoire naturelle, Département d'herpétologie et d'ichtyologie, route de Malagnou 1, case postale 6434, CH-1211 Genève 6, Suisse. [Sonia.Fisch-Muller@ville-ge.ch]

(2) Université de Genève, Département de génétique et évolution, Sciences III, quai E. Ansermet 30, CH-1211 Genève 4, Suisse. [juan.montoya@unige.ch]

(3) Université Claude Bernard Lyon 1, Laboratoire de biométrie et de biologie évolutive, CNRS, UMR 5558, 43 bd du 11 Novembre 1918, 69622 Villeurbanne CEDEX, France. [dray@biomserv.univ-lyon1.fr]

(4) University of Suriname, Center for Agricultural Research in Suriname CELOS and Department of Biology, POB 9212, Paramaribo, Suriname. [fisheco@celos.sr.org]

(5) SCRIBE-INRA, Campus de Beaulieu, 35042 Rennes CEDEX, France. [Pierre-Yves.Lebail@rennes.inra.fr]

\* Corresponding author [Raphael.Covain@ville-ge.ch]

cies, representing one quarter of the Neotropical fish diversity, among which 700 are considered endemic (source WWF: [http://wwf.panda.org/about\\_our\\_earth/ecoregions/guianan\\_freshwater.cfm](http://wwf.panda.org/about_our_earth/ecoregions/guianan_freshwater.cfm)). For the Guiana Shield Vari and Ferraris (2009) listed 1,168 valid species of fish distributed in 15 orders, and 49 families. Therein, excluding lowlands species, they reported 429 species in Guyana, 309 in Suriname with 34% species overlap between these two countries, and 298 in French Guiana with 46% of shared species between French Guiana and Suriname. Planquette *et al.* (1996) listed 429 species in French Guiana alone. Among this tremendous diversity, 80 valid species of Loricariidae were recorded from the three Guianas (Vari and Ferraris, 2009), including 38 species in Guyana, 45 species in Suriname, and 25 species in French Guiana.

The Loricariidae is a highly diversified catfish family comprising about 1,000 species, characterized by a depressed body covered by bony plates, a single pair of maxillary barbels, and by an important modification of the mouth structure into a sucker disk. Recent investigations conducted by the authors in Guyana, Suriname, and French Guiana revealed the presence of several new species and populations of Loricariidae belonging to the tribe Harttiini.

The Harttiini represents a group of rheophilic fishes mainly distributed in the eastern part of South America, in rivers flowing across Brazilian and Guiana Shields. Most inhabit the main stream of rivers over rocky and sandy bottoms, in swift currents where the water is clear and well oxygenated. The systematics of Harttiini has remained confused until now, due to their low morphological diversity. Isbrücker (1979) defined the Harttiini as having the dorsal fin originating approximately opposite to the pelvic-fin origin, the caudal fin with 12 (rarely 11) soft rays, no orbital notch, and little variability in tooth and lip structures. In the same work, Isbrücker and Nijssen described *Cteniloricaria*, distinguishing it from *Harttia* by a slender body shape, a more deeply forked caudal fin, and the abdomen wholly covered by medium sized plates. Isbrücker (1979) placed *Sturisoma*, *Harttia*, *Lamontichthys*, *Harttiella*, *Pterosturisoma*, *Cteniloricaria*, *Sturisomatichthys*, and *Metaloricaria* within Harttiini. Montoya-Burgos *et al.* (1998) proposed the first molecular phylogeny of the family Loricariidae, and provided evidence that the Harttiini, as defined by Isbrücker (1979), was not a monophyletic assemblage. Isbrücker (*in* Isbrücker *et al.*, 2001) described *Quiritixys* only based on the unusual sexual dimorphism of *Harttia leiopleura*. Rapp Py-Daniel and Oliveira (2001) described seven species of *Harttia*, and put *Cteniloricaria* in the synonymy of *Harttia* mainly based on the characteristics of *H. fowleri* but without consulting the type species: *Cteniloricaria platystoma*. Ferraris (2003, 2007) maintained the validity of *Cteniloricaria*, and put *Quiritixys* in the synonymy of *Harttia*. Provenzano *et al.* (2005), Covain *et al.* (2006), and Covain and Fisch-

Muller (2007) maintained the synonymy of *Cteniloricaria* and *Harttia*. The latter also tentatively placed the monotypic genus *Harttiella* into Harttiini, suggesting *Harttiella* as a dwarf form closely related to *Harttia*. Covain *et al.* (2008) proposed the first molecular phylogeny of the subfamily, and redefined the systematics of the Loricariinae. They placed *Metaloricaria* within Loricariina, and *Lamontichthys*, *Farlowella*, *Sturisoma*, and *Sturisomatichthys* within Farlowellina, both subtribes belonging to the tribe Loricariini. In the same work, they restricted Harttiini to *Harttia*. The Harttiini comprises currently 23 valid species, including eight species distributed on the Guiana Shield (including part of Brazil and Venezuela). Within the Guianas (Guyana, Suriname, and French Guiana), six valid species of Harttiini are recorded, including five species of *Harttia*, and one *Harttiella*.

*Harttiella crassicauda* was initially collected by Geijskens and Creutzberg in the Nassau Mountains during the 1948-1949 Suriname expedition (Bakker and Lanjouw, 1949; Boeseman, 1953). This unusual species was described as a representative of *Harttia* by Boeseman (1953), but due to its particular morphology, Boeseman (1971) created the genus *Harttiella* to accommodate the species. *Harttiella* was characterized by a depressed body shape, broad head, body, and caudal peduncle, the absence of lateral and predorsal keels, the strongly spiny body plates, the naked belly, and a thick caudal peduncle (Boeseman, 1971). The species is only known from the Nassau Mountains in Suriname, an isolated plateau (570 meters above mean sea level) in Northeastern Suriname. Geijskens and Creutzberg described the habitat of *Harttiella crassicauda* as a small forest creek on top of Nassau Mountains, with a rocky bottom covered with sand and stones, and some falls. They located the creek as a tributary of the Marowijne River, but without providing more details. Mol and Ouboter (2004) mentioned that *H. crassicauda* was at risk of extinction or possibly already extinct because of mining activities in Nassau Mountains. However, in 2005 Mol and co-workers collected the species for the second time, 56 years after its original collection. At the same time, they noted that *H. crassicauda* was still an endangered species due to potential degradation of its habitat by both small and large scale mining, and its restricted distribution in a single creek (Mol *et al.*, 2007). By allowing a better grasp of its morphology and ecology, the rediscovery of *H. crassicauda* led to the discovery of additional populations potentially belonging to *Harttiella* in French Guiana.

In the present study, we provide a global assessment on the diversity of Harttiini within the Guianas that includes all species and populations collected during the last decade. Based on a multi-table approach integrating genetics through DNA barcodes, morphometry, and ecology-distribution of the different species and populations, the systematics of Harttiini is revised, their main evolutionary trends are revealed, and new taxa are described.

## MATERIAL AND METHODS

### Morphometry

This study was based on 622 measured specimens and included all populations and species of Harttiini collected from the Guianas. Part of this material was previously analysed by Covain *et al.* (2006), and is not listed again. The additional material, including type specimens of *H. fowleri*, *H. guianensis*, *H. crassicauda*, *H. platystoma*, and *H. maculata*, was deposited in the Muséum d'histoire naturelle, Geneva (MHNG), the Muséum national d'Histoire naturelle, Paris (MNHN), the National Museum of Natural History-Naturalis, Leiden (RMNH), the British Museum of Natural History, London (BMNH), the Centre for the Study of Biological Diversity, University of Guyana, Georgetown (CSBD), and the Academy of Natural Sciences, Philadelphia (ANSP).

In the list of measured material, institutional acronyms and catalogue numbers are presented first, followed by the number of specimens in the lot, locality, collector and date of collection. Institutional acronyms follow Fricke and Eschmeyer (2010). To prevent artificial groupings, the different populations collected in different basins were considered independently. The taxonomy followed Covain *et al.* (2006), and the abbreviations used in the different analyses are provided between square brackets.

*H. platystoma*: Guyana, Essequibo River drainage [Hplat]. - BMNH 1866.8.14.124 lectotype of *Loricaria platystoma* Günther, 1868, Surinam (?); MHNG 2651.080 (3), CSBD uncat. (2, ex MHNG 2651.080), Burro-Burro River, 2.5 km upstream of the confluence with the Siparuni River, Montoya-Burgos *et al.*, 2 Nov. 2004; MHNG 2650.093 (2), CSBD uncat. (3, ex MHNG 2650.093), Jamas Rapids at Kurupukari Cross, Montoya-Burgos *et al.*, 31 Oct. 2004; MHNG 2651.035 (3), CSBD uncat. (2, ex MHNG 2651.035), upper Rupununi, near Dadanawa ranch, Montoya-Burgos *et al.*, 26 Oct. 2004; MHNG 2650.090 (2), CSBD uncat. (1, ex MHNG 2650.090), Essequibo River, Kurupukari Cross, Montoya-Burgos *et al.*, 31 Oct. 2004; MHNG 2650.082 (2), CSBD uncat. (3, ex MHNG 2650.082), Siparuni River, just downstream of Georges Creek, Montoya-Burgos *et al.*, 2 Nov. 2004; ANSP 182390 (3), Essequibo River, Kurupukari Cross, Sabaj *et al.*, 24 Oct. 2002; ANSP 182341 (6), Kuyuwini River, 48.3 km E of Kuyuwini Landing, 182 km SE of Lethem, Sabaj *et al.*, 6 Nov. 2003.

*H. maculata*: Suriname, Corantijn River drainage [HmacC]. - RMNH 26381 holotype of *Parasturisoma maculata* Boeseman, 1971, upper Corantijn River basin, Sipaliwini, near airstrip; MHNG 2704.021 (1), Corantijn River, Sir Walter Raleigh's Falls, Montoya-Burgos *et al.*, 15 Oct. 2007; MHNG 2704.016 (6), MHNG 2704.017 (7), MHNG 2704.019 (3), Sipaliwini River, Paikali Rapids, Montoya-Burgos *et al.*, 14 Oct. 2007; MHNG 2704.015 (2), Sipaliwini River, Yavi Sowa Rave Creek, Montoya-Burgos *et al.*, 14 Oct. 2007; MHNG 2704.022 (4), Curuni River, at Sir Walter Raleighwallen, Montoya-Burgos *et al.*, 15-16 Oct. 2007; MHNG

2704.027 (5), Sipaliwini River, in rapids, Montoya-Burgos *et al.*, 22 Oct. 2007; MHNG 2704.026 (7), Manicouni River, at confluence with Sipaliwini River, Montoya-Burgos *et al.*, 20 Oct. 2007; MHNG 2704.024 (10), Sipaliwini River, 15 min upstream of Kwamalasamutu village, Montoya-Burgos *et al.*, 17 Oct. 2007; MHNG 2704.020 (11), Corantijn River, in Sir Walter Raleighvalle, Montoya-Burgos *et al.*, 15 Oct. 2007. Suriname, Suriname River drainage [HmacS]. - MHNG 2673.073 (1), Gran Rio River, Assigon, Montoya-Burgos *et al.*, 31 Oct. 2005; MHNG 2671.047 (1), Gran Rio River, Cajana around 200 m downstream of Kossindo village, Montoya-Burgos *et al.*, 2 Nov. 2005; MHNG 2673.026 (3), Gran Rio River, Cajana Creek, Montoya-Burgos *et al.*, 2 Nov. 2005; MHNG 2674.003 (5), Gran Rio River, Awaradam, Montoya-Burgos *et al.*, 29 Oct. 2005. French Guiana-Suriname, Maroni/Marowijn River drainage [HmacM]. MHNG 2643.001 (1/2), Tampoc River, Pièrkourou Falls, Fisch-Muller *et al.*, 13 Oct. 2000; MHNG 2683.037 (1), Crique Voltaire, Voltaire Falls, Fisch-Muller *et al.*, 13 Nov. 2006; MHNG 2683.027 (3), Crique Voltaire, Voltaire camp, Fisch-Muller *et al.*, 12 Nov. 2006; MHNG 2643.013 (1), Tampoc River, Pièrkourou Falls, Fisch-Muller *et al.*, 13 Oct. 2000; MHNG 2643.029 (1), Tampoc River, st. 6, Le Bail and Keith, 17 Nov. 1998; MHNG 2643.027 (4/5), Grand Inini River, in reach, Le Bail *et al.*, 28 Sept. 1997; MHNG 2717.042 (26), Paloemeu River, tributary of Tapanahony River at Weyu camp, Montoya-Burgos *et al.*, 28-30 Oct. 2008. French Guiana, Mana River drainage [HmacMn]. MHNG 2700.054 (1), Crique Aya, 400 m downstream of Aya camp, Montoya-Burgos and Melki, 28 Nov.-4 Dec. 2007.

*H. surinamensis*: Suriname, Suriname River drainage [Hsur]. - MHNG 2674.007 (27), Gran Rio River, Awaradam, Montoya-Burgos *et al.*, 29 Oct. 2005; MHNG 2674.042 (9), Gran Rio River, Cajana around 150 m downstream of Kossindo village, Montoya-Burgos *et al.*, 28 Oct. 2005; MHNG 2673.014 (5), Gran Rio River, Cajana near Kossindo, Montoya-Burgos *et al.*, 2 Nov. 2005; MHNG 2673.033 (13/33), Gran Rio River, Cajana Creek, Montoya-Burgos *et al.*, 2 Nov. 2005.

*H. fowleri*: French Guiana, Oyapock River drainage [Hfow]. - MNHN 1901-0372 holotype of *Oxyloricaria fowleri* Pellegrin, 1908, Camopi River; MHNG 2680.091 (18), Oyapock River, Alikoto Falls, Covain *et al.*, 3 Nov. 2006; MHNG 2643.023 (2), Oyapock River, upstream of Maripa Falls, Fisch-Muller *et al.*, 20 Oct. 1999; MHNG 2681.091 (1), Oyapock River, at mouth of Crique Mouloukoulou, Covain *et al.*, 4 Nov. 2006.

*H. guianensis*: French Guiana, Approuague River drainage [HguiAp]. MNHN 1998-0395 holotype of *Harttia guianensis* Rapp Py-Daniel & Oliveira, 2001, Approuague River, Saut Athanase (52°1'W-4°11'N); MNHN 1998-0396 (2), paratypes, same data as holotype; MHNG 2621.097 (3/7), Approuague River, Mapaou Falls, Weber *et al.*, 4 Nov. 2001; MHNG 2662.093 (4), Arataï River, Pararé Falls, Fisch-Muller *et al.*, 21 Nov. 2003; MHNG 2662.099 (1), Arataï River, Crique Nourague, Fisch-Muller *et al.*, 21 Nov. 2003; MHNG 2662.100 (2), Arataï River, Crique Nourague, Fisch-Muller *et al.*, 22 Nov. 2003; MHNG 2662.091 (3), Arataï River, Grand Japigny Falls, Fisch-Muller *et al.*, 22 Nov.



2003. French Guiana, Maroni River drainage [HguiMr]. MHNG 2643.019 (1), Maroni River, Creek near power station of Antecume Pata, Fisch-Muller and Weber, 20 Oct. 2000; MHNG 2643.010 (3), Litany River, W-SW Falls from Antecume Pata, Jégu *et al.*, 24 Oct. 2000. French Guiana, Sinnamary River drainage [HguiSi]. MHNG 2661.009 (5), Sinnamary River, Deux Roros Falls, Vigouroux, 17 Nov. 2004; MHNG 2680.053 (3/34), Sinnamary River, Takari Tanté Falls, Vigouroux, 15.10.2003.

*H. crassicauda*: Suriname, Marowijn River drainage [Hcras]. RMNH 19418 (8/15) holotype and paratypes of *Harttia crassicauda* Boeseman, 1953, Nassau Mountains, in creek, Suriname; MHNG 2674.051 (11), MHNG 2674.053 (3), Nassau Mountains, Paramaka Creek N1, Mol, 2 Nov. 2005; MHNG 2679.098 (4/5), Nassau Mountains, Paramaka Creek, Mol, Apr. 2006.

Unidentified Harttiini: *H. aff. maculata* [Haffmac]. MHNG 2704.030 (12), Sipaliwini Savannah, Trio Amerindian territory, Suriname-Brazil border, Four Brothers Mountains, Paru de Oeste River, Trio tribe, 20-21 Oct. 2007. *H. aff. trombetensis* [Hafftrom]. MHNG 2704.029 (27), Sipaliwini Savannah, Trio Amerindian territory, Suriname-Brazil border, Four Brothers Mountains, Paru de Oeste River, Trio tribe, 20-21 Oct. 2007. *H. sp.* Coppename [HCopp]. MHNG 2690.012 (7), Suriname, Coppename River at Raleighvallen, Mol, 29 Nov. 2006; MHNG 2690.013 (17), Suriname, Coppename River at Raleighvallen, Mol, 30 Nov. 2006. *H. sp.* Aratai [HArata]. MHNG 2723.094 (16), French Guiana, Approuague River, Balenfois Mountains, Crique Cascades, Gaucher, Feb. 2008. *H. sp.* Atachi Bakka [Hatach]. MHNG 2723.093 (6), French Guiana, Maroni River, Atachi Bakka Mountains, Gaucher, Jun. 2009. *H. sp.* Kotika [HCotic]. MHNG 2695.059 (80), French Guiana, Maroni River, Kotika Mountains, Tostain, 05 Sept. 2007. *H. sp.* Lucifer [Hlucif]. MHNG 2721.088 (10), French Guiana, Mana River, Lucifer Mountains, West of Crique Cascade, Montoya-Burgos and Fischer, 10 Feb. 2010; MHNG 2721.091 (7), French Guiana, Mana River, Lucifer Mountains, headwater of flowing toward Citron, Montoya-Burgos and Fischer, 11 Feb. 2010. *H. sp.* Mana [HMana]. MHNG 2699.070 (45/53), French Guiana, Mana River, Trinité Mountains, Crique Baboune, Crique Aya around 100 m in front of Aya Camp, Montoya-Burgos and Melki, 28 Nov.-04 Dec. 2007; MHNG 2699.098 (4), French Guiana, Trinité Mountains, Mana River, Crique Aya at foot of inselberg, Montoya-Burgos and Melki, 28 Nov.-04 Dec. 2007. *H. sp.* Orapu [HORap]. MHNG 2682.055 (10), French Guiana, Tortue Mountains, Orapu River, Crique Grillon at ONF camp, Covain *et al.*, 8 Nov. 2006; MHNG 2724.002 (1), French Guiana, Tortue Mountains, Orapu River, Crique Grillon at ONF camp, Vigouroux *et al.*, 7 Nov. 2003. *H. sp.* Saul [Hsaul]. MHNG 2712.085 (6), French Guiana, Maroni River, Galbao Mountains, Crique Limonade, Tostain, 18 Mar. 2008. *H. sp.* Sinnamary [HSinna]. MHNG 2723.095 (1, ex MHNG 2643.030), French Guiana, Sinnamary River, Crique Cœur Maroni, Le Bail *et al.*, 15 Oct. 1982 or 02 Feb. 1983. *H. sp.* Trinité [Htrinit]. MHNG 2713.087 (5), French Guiana, Sinnamary River, Tabular Mountain of Trinité massif, Crique Grand Leblond, Tostain and Ravet, 6 Oct. 2009.

All specimens were measured with a digital calliper to the nearest 0.01 mm. The measurements and counts follow Covain *et al.* (2006) except for: (1) the premaxillary ramus length, due to difficulty and inaccuracy of the measurement; (2) the measurements related to the tail characteristics (total length, upper and lower caudal-spine lengths, and minimum caudal-fin length) due to numerous broken tails; and (3) the angular measurements of the snout  $\alpha$  and  $\beta$  because these two measurements are highly correlated to the head depth and cleithral width respectively, and increased consequently redundancy in the dataset. While these seven measurements were excluded, we added the thoracic and abdominal lengths according to Isbrücker (1973), and the distances between the anus and the tip of the snout, and the anus and the insertion of the anal, pelvic and pectoral fins. The dataset therefore included 29 continuous morphometric variables, and 4 discrete meristic variables. The list of variables is provided in table I. Specimens smaller than 20 mm were excluded from the analyses to minimize the bias introduced by allometric growth. Because morphometric data are highly correlated between them, missing data (representing less than 0.45% of the whole data set) were estimated for specimens belonging to a given population using the least squares method with the standard length (SL) used as explanatory variable.

In order to highlight the morphological structure of the species and populations under study, the data were subjected to multivariate analyses. Prior to the analyses, all measurements were standardized by the SL and log transformed. This transformation, equivalent to the additive log ratio of Aitchinson (1986), controls for size effect, preserves and linearizes allometric growth, and prevents spurious correlations of simple ratios (Atchley *et al.*, 1976; Corrucini, 1977; Albrecht, 1978; Atchley and Anderson, 1978; Dodson, 1978; Hills, 1978). The final table included data on 618 specimens of Harttiini, from 23 different populations, and 32 columns. This table was then centred and reduced to allow comparison of variables expressed in different units (here no unit for log ratio transformed measurements, and number of objects for the meristic data), and submitted to a principal components analysis (PCA) to reveal its structuring. PCA was performed with the ade4 1.4-14 (Dray and Dufour, 2007) and ade4TkGUI 0.2-5 (Thioulouse and Dray, 2007) packages in R 2.10.1 (R Development Core Team, 2009).

## Genetics

To provide further evidence for the assessment of the global diversity of the Guianese Harttiini, the standard 648-bp 5' region of the cytochrome *c* oxidase I (COI) mitochondrial gene used for DNA barcodes was amplified. This DNA marker was sequenced in a total of 42 specimens representing 21 populations and comprising at least one specimen per population. The list of material used for this analysis is provided in table II. Ethanol preserved tissue samples are deposited in



MHNG. Total genomic DNA was extracted with the DNeasy Tissue Kit (Qiagen) following the instructions of the manufacturer. The PCR amplifications were carried out using the Taq PCR Core Kit (Qiagen). The primers used were Fish-F1 and Fish-R1 (Ward *et al.*, 2005). The amplifications were performed in a total volume of 50  $\mu$ l, containing 5  $\mu$ l of 10x reaction buffer, 1  $\mu$ l of dNTP mix at 10mM each, 1  $\mu$ l of each primer at 10  $\mu$ M, 0.2  $\mu$ l of *Taq* DNA Polymerase equivalent to 1 unit of Polymerase per tube, and 1  $\mu$ l of DNA. Cycles of amplification were programmed with the following profile: (1) 3 min. at 94°C (initial denaturing), (2) 35 sec. at 94°C, (3) 30 sec. at 54°C, (4) 50 sec. at 72°C, and (5) 5 min. at 72°C (final elongation). Steps 2 to 4 were repeated 39 times. PCR products were purified with the High Pure PCR Product Purification Kit (Roche). Sequencing reactions were performed with the Big Dye Terminator Cycle Sequencing Ready Reaction 3.1 Kit (Applied Biosystems) following instructions of the manufacturer, and were loaded on an automatic sequencer 3100-Avant Genetic Analyzer (Applied Biosystems, Perkin-Elmer). The sequences were deposited in GenBank, and accession numbers are provided in table II.

The DNA sequences were edited and assembled using BioEdit 7.0.1 (Hall, 1999), and aligned manually since the coding COI gene aligned unambiguously in a single block. The GC content and base composition were computed using the seqinr 2.0-9 package (Charif and Lobry, 2007) in R, and usual tests of homogeneity of nucleotide frequencies and substitution saturation (Xia *et al.*, 2003) were performed using Dambe 4.5.56 (Xia and Xie, 2001). The alignment was secondarily converted into a distance matrix using the Kimura 2 Parameters (K2P) metrics (Kimura, 1980) as implemented in ape 2.5 (Paradis *et al.*, 2004; Paradis, 2006) in R, to evaluate sequence divergence. A Neighbour Joining (NJ) tree (Saitou and Nei, 1987) was reconstructed on this distance matrix to provide a cluster ordination of the species. This ordination did not correspond to a phylogeny, but rather to a group assignment using distances between sequences (whatever their evolutionary history). The NJ algorithm has the advantage over other agglomerative partitioning methods to preserve distances into branch lengths, and consequently to not enforce artificially the grouping of species (e.g., using a mean distance between clusters). To estimate robustness of the groupings, a nonparametric bootstrap analysis (Efron, 1979) was performed following Felsenstein (1985) methodology using 9,999 pseudoreplicates. In addition, a levelplot graph allowing a graphical representation of the distance matrix was computed using the lattice 0.18-3 (Sarkar, 2010) and colorRamps 2.3 (Keitt, 2009) packages in R. In a second analysis, the distance matrix was explored by a principal coordinate analysis (PCoA) (Gower, 1966) using Cailiez (1983) correction for non Euclidian distance matrices, to reveal its structuring onto axes. This analysis provides a tree-free representation of the distance matrix, where the

pairwise distances between OTUs are equal to the genetic pairwise distances of the matrix.

### Ecology and distribution

To highlight the environmental parameters structuring the different species and populations, four environmental variables and three distributional variables were analysed. Environmental parameters [pH, conductivity, temperature, and habitat (main channel of rivers or creeks)] and distributional information (latitude, longitude, and altitude) were obtained from the field, the literature (Horeau *et al.*, 1998; Négrel and Lachassagne, 2000; de Mérona, 2005; Sondag *et al.*, 2010), or generously provided by co-workers (B. de Mérona, IRD Cayenne; P. Gaucher, CNRS Guyane; R. Vigouroux, Hydreco Guyane; and O. Tostain, Ecobios Cayenne). Environmental data extracted from the literature were included only if specimens examined by Covain *et al.* (2006) were from exactly the same localities. The final table included 88 rows, corresponding to 19 populations and species, of which nine contained missing values. This dataset was submitted to multivariate analyses using the Non-linear Iterative Partial Least Squares (NIPALS) algorithm (Wold, 1966; Dray *et al.*, 2003) as implemented in ade4 1.4-14. This algorithm allows for PCA analysis on a table with missing data, and does not require the deletion of rows or variables containing missing values. The algorithm is based on successive linear regressions using an iterative procedure (Tenenhaus, 1998) and reconstructs the complete table (i.e., estimation of missing values) for further analyses.

### Multi-table analysis

To synthesize the various types of information concerning Harttiini presented above (genetics, morphometry, and distribution-ecology), and identify the possible common structures present within all data sets, the three tables were linked by a multiple co-inertia analysis (MCOA) (Chessel and Hanafi, 1996). Prior to the analysis, all tables were restricted to the subset of populations ( $n = 19$ ) for which the three types of information were available. Each of the three reduced tables was reanalysed separately (PCoA for the genetic data, and PCA for the morphometric and ecological data) to reveal their structuring. Within-population variability was eliminated by the computation of average values for each population. The table reconstructed by the NIPALS algorithm was used for the ecological table. A first assessment of a possible link between the three tables was obtained using the Congruence Among Distance Matrices (CADM) test (Legendre and Lapointe, 2004) as implemented in ape 2.5 in R. The CADM test is a generalization of the Mantel test (Mantel, 1967) to test the null hypothesis of incongruence between several distance matrices. Additionally, an *a posteriori* procedure allows testing for the incongruence of a single distance matrix with respect to the other ones. A

Table I. - Descriptive morphometrics and meristics of all Guianese Harttiini. Morphometric data expressed as percents of standard length (SL) or head length (HL). Abbreviations of the different morphometric variables used in the analyses are provided between square brackets. N: number of specimens measured. Computed statistics include holotype.

N	<i>Cteniloricaria platystoma</i>			<i>Cteniloricaria napova</i>			<i>Harttiella crassicauda</i>		
	range	mean $\pm$ sd	lectotype	range	mean $\pm$ sd	holotype	range	mean $\pm$ sd	holotype
Standard length (SL)	38.36 - 180.26	90.05 $\pm$ 41.36	171.40	71.04 - 128.73	111.83 $\pm$ 15.36	113.20	24.09 - 47.96	32.40 $\pm$ 5.37	47.96
Percents of SL									
Head length [Ltet]	18.48 - 23.93	21.11 $\pm$ 1.19	19.59	20.38 - 24.62	21.36 $\pm$ 1.09	21.23	23.69 - 28.12	25.83 $\pm$ 1.17	23.69
Predorsal length [LpreDo]	27.85 - 32.66	29.91 $\pm$ 0.90	29.39	29.97 - 31.41	30.91 $\pm$ 0.38	31.05	36.99 - 39.69	38.56 $\pm$ 0.74	36.99
Postdorsal length [LpostDo]	58.48 - 64.75	61.60 $\pm$ 1.14	61.34	59.61 - 62.08	60.73 $\pm$ 0.74	59.62	46.16 - 49.79	48.05 $\pm$ 0.92	49.79
Caudal peduncle length [LpostAn]	47.95 - 55.82	51.74 $\pm$ 1.17	50.15	49.34 - 53.00	51.03 $\pm$ 0.90	50.43	32.77 - 39.79	36.14 $\pm$ 1.66	35.53
Abdominal length [Labd]	8.04 - 18.52	16.60 $\pm$ 1.05	17.91	15.79 - 17.32	16.81 $\pm$ 0.45	16.27	17.49 - 22.17	19.96 $\pm$ 1.33	20.52
Thoracic length [Lthor]	11.91 - 19.11	15.99 $\pm$ 0.96	15.85	14.89 - 17.09	16.06 $\pm$ 0.68	15.85	19.46 - 25.21	21.81 $\pm$ 1.65	22.62
Pectoral spine length [Lpect]	18.11 - 28.38	21.65 $\pm$ 2.42	27.12	19.56 - 22.10	20.97 $\pm$ 0.83	22.10	21.66 - 27.15	24.72 $\pm$ 1.73	24.96
Pelvic spine length [Lpelv]	16.10 - 21.26	18.10 $\pm$ 1.01	19.05	16.90 - 18.22	17.53 $\pm$ 0.42	17.86	17.76 - 25.18	22.86 $\pm$ 1.64	22.96
Dorsal spine length [Ldo]	17.84 - 36.27	23.66 $\pm$ 3.52	36.27	20.76 - 23.88	22.18 $\pm$ 0.90	22.92	17.33 - 27.01	23.76 $\pm$ 2.55	17.33
Anal spine length [Lan]	8.01 - 16.91	14.37 $\pm$ 1.22	15.72	13.63 - 15.72	14.77 $\pm$ 0.67	14.74	11.98 - 18.26	16.23 $\pm$ 1.62	13.62
Anus to pelvic-fin origin length [Dampelv]	7.22 - 10.14	8.74 $\pm$ 0.60	9.17	8.47 - 9.72	9.00 $\pm$ 0.34	9.22	7.78 - 14.10	10.96 $\pm$ 1.72	14.10
Anus to pectoral-fin origin length [Dampect]	19.29 - 25.81	23.31 $\pm$ 0.93	23.50	22.44 - 25.39	23.92 $\pm$ 0.89	23.78	27.89 - 36.62	31.85 $\pm$ 2.26	35.43
Anus to anal-fin origin length [Danan]	7.25 - 10.39	8.88 $\pm$ 0.52	10.26	8.02 - 9.70	8.94 $\pm$ 0.48	8.26	7.97 - 12.79	9.74 $\pm$ 1.37	9.07
Anus to tip of snout length [Danmus]	33.84 - 39.68	36.81 $\pm$ 0.92	35.96	36.16 - 37.96	37.09 $\pm$ 0.58	37.38	44.20 - 50.44	48.09 $\pm$ 1.93	49.37
Body width at dorsal-fin origin [LcorDo]	12.64 - 17.31	14.62 $\pm$ 0.91	15.54	13.85 - 15.89	15.17 $\pm$ 0.61	15.41	16.80 - 22.74	20.06 $\pm$ 1.61	21.96
Body width at anal-fin origin [LcorAn]	8.86 - 14.49	12.02 $\pm$ 1.06	13.03	10.75 - 12.90	12.06 $\pm$ 0.54	12.47	11.72 - 15.34	13.71 $\pm$ 1.14	14.95
Body width at eighth postdorsal plate [l8]	6.53 - 11.30	9.34 $\pm$ 0.97	10.05	8.13 - 10.07	8.85 $\pm$ 0.58	8.52	9.30 - 13.41	11.48 $\pm$ 0.94	13.41
Body width at fourteenth postdorsal plate [l14]	2.89 - 4.83	3.96 $\pm$ 0.47	4.47	3.51 - 4.61	4.01 $\pm$ 0.33	3.85	4.14 - 6.73	5.27 $\pm$ 0.75	6.73
Body depth at dorsal-fin origin [Hcor]	6.91 - 11.84	9.16 $\pm$ 1.00	9.71	8.60 - 11.08	10.04 $\pm$ 0.69	10.24	8.51 - 13.60	11.41 $\pm$ 1.41	10.20
Minimum caudal peduncle depth [HminPC]	0.94 - 1.39	1.13 $\pm$ 0.10	1.27	1.05 - 1.18	1.11 $\pm$ 0.04	1.12	3.88 - 5.59	4.86 $\pm$ 0.43	5.36
Head length (HL)	8.96 - 34.90	18.60 $\pm$ 7.68	33.57	17.49 - 27.14	23.76 $\pm$ 2.63	24.03	6.68 - 11.36	8.32 $\pm$ 1.10	11.36
Percents of HL									
Snout length [Lmus]	47.84 - 59.57	53.64 $\pm$ 3.05	58.62	43.11 - 55.14	52.04 $\pm$ 3.06	55.14	55.48 - 62.82	57.93 $\pm$ 1.58	58.80
Nostril to tip of snout length [LnarBM]	32.16 - 44.80	39.16 $\pm$ 2.70	43.25	31.05 - 38.37	36.86 $\pm$ 1.93	38.37	37.59 - 43.67	40.90 $\pm$ 1.51	40.76
Cleithral width [lret]	71.13 - 95.25	82.81 $\pm$ 4.95	87.58	68.32 - 87.40	82.20 $\pm$ 4.81	86.23	59.83 - 110.61	97.14 $\pm$ 9.54	110.48
Distal end of operculum to tip of snout length [OpercBM]	70.51 - 82.10	77.87 $\pm$ 2.11	76.74	67.18 - 80.05	76.51 $\pm$ 3.44	80.02	78.57 - 90.63	84.40 $\pm$ 2.79	86.80
Maximum orbital diameter [Dmoel]	18.38 - 28.33	23.47 $\pm$ 2.18	18.38	21.56 - 23.70	22.60 $\pm$ 0.62	22.43	14.93 - 20.17	17.21 $\pm$ 1.20	15.85
Interorbital width [Distintorb]	18.80 - 25.60	22.50 $\pm$ 1.11	23.41	18.12 - 23.26	21.51 $\pm$ 1.29	21.81	30.63 - 38.23	35.58 $\pm$ 1.69	37.76
Head depth [Htet]	32.99 - 51.80	40.83 $\pm$ 2.85	42.06	35.51 - 44.35	42.21 $\pm$ 2.37	43.20	41.17 - 51.05	45.79 $\pm$ 2.79	43.49
Head depth at internostri [Hintnar]	23.70 - 37.05	29.69 $\pm$ 2.55	32.38	22.64 - 31.62	28.75 $\pm$ 2.44	28.80	29.00 - 37.70	33.89 $\pm$ 2.22	33.98
Meristic									
Number of premaxillary teeth [Nbdtissup]	21 - 73	40 $\pm$ 12	64	35 - 58	47 $\pm$ 6	44	20 - 43	29 $\pm$ 5	31
Number of dentary teeth [Nbdtisinf]	17 - 64	38 $\pm$ 11	64	31 - 48	41 $\pm$ 4	39	16 - 39	28 $\pm$ 5	24
Number of plates in the lateral series [Nblongit]	28 - 31	30 $\pm$ 1	29	30 - 30	30 $\pm$ 0	30	24 - 27	26 $\pm$ 1	25
Number of lateral abdominal plates [Nbseutvent]	5 - 14	8 $\pm$ 2	7	7 - 11	9 $\pm$ 1	10	4 - 7	5 $\pm$ 1	6

Table I. - Continued.

	<i>Harttiella pilosa</i>			<i>Harttiella parva</i>			<i>Harttiella intermedia</i>		
	range	mean $\pm$ sd	holotype	range	mean $\pm$ sd	holotype	range	mean $\pm$ sd	holotype
N									
Standard length (SL)	22.69 - 40.27	35.05 $\pm$ 6.25	39.91	23.73 - 31.27	28.50 $\pm$ 2.65	29.54	21.39 - 34.67	27.60 $\pm$ 5.81	34.67
Percents of SL									
Head length [L <sub>het</sub> ]	22.14 - 27.06	23.74 $\pm$ 1.35	23.55	24.27 - 27.82	26.12 $\pm$ 1.34	25.22	24.69 - 27.77	26.18 $\pm$ 1.12	26.02
Predorsal length [L <sub>preDo</sub> ]	33.90 - 37.33	35.27 $\pm$ 0.93	35.78	37.05 - 38.91	37.72 $\pm$ 0.89	37.14	36.37 - 38.76	37.93 $\pm$ 1.07	38.62
Postdorsal length [L <sub>postDo</sub> ]	51.94 - 55.85	53.60 $\pm$ 1.45	52.09	49.55 - 53.47	51.77 $\pm$ 1.59	51.15	48.90 - 53.44	51.37 $\pm$ 1.86	50.74
Caudal peduncle length [L <sub>postAn</sub> ]	42.34 - 45.46	43.94 $\pm$ 0.90	43.72	38.66 - 41.93	40.36 $\pm$ 1.06	38.66	40.67 - 43.96	42.35 $\pm$ 1.44	40.67
Abdominal length [L <sub>abd</sub> ]	17.21 - 19.28	18.09 $\pm$ 0.68	17.94	16.01 - 18.45	17.75 $\pm$ 0.91	18.45	16.83 - 20.39	18.43 $\pm$ 1.37	20.39
Thoracic length [L <sub>thor</sub> ]	14.46 - 24.17	18.99 $\pm$ 2.35	19.42	19.13 - 23.74	22.47 $\pm$ 1.69	23.22	18.52 - 20.97	19.75 $\pm$ 0.97	20.45
Pectoral spine length [L <sub>pect</sub> ]	19.16 - 22.51	21.14 $\pm$ 0.98	21.40	22.51 - 25.07	24.00 $\pm$ 0.95	24.92	23.16 - 25.12	24.06 $\pm$ 0.84	25.12
Pelvic spine length [L <sub>pelv</sub> ]	19.89 - 21.03	20.55 $\pm$ 0.36	20.87	21.09 - 23.05	22.05 $\pm$ 0.77	23.05	19.52 - 21.81	20.99 $\pm$ 1.02	21.75
Dorsal spine length [L <sub>do</sub> ]	19.30 - 22.36	20.98 $\pm$ 0.78	20.65	22.08 - 26.61	24.80 $\pm$ 1.68	26.61	17.51 - 27.49	23.83 $\pm$ 3.74	24.66
Anal spine length [L <sub>an</sub> ]	14.40 - 18.80	15.73 $\pm$ 1.27	16.14	14.50 - 18.11	15.95 $\pm$ 1.36	18.11	11.79 - 18.56	16.00 $\pm$ 2.54	16.47
Anus to pelvic-fin origin length [D <sub>ampelv</sub> ]	8.34 - 12.20	10.55 $\pm$ 1.11	11.05	7.78 - 11.07	9.29 $\pm$ 1.42	11.07	10.12 - 12.34	11.31 $\pm$ 1.01	12.34
Anus to pectoral-fin origin length [D <sub>ampect</sub> ]	23.50 - 33.53	28.38 $\pm$ 2.75	30.04	26.76 - 31.55	29.23 $\pm$ 1.81	31.55	28.19 - 31.76	29.16 $\pm$ 1.51	31.76
Anus to anal-fin origin length [D <sub>anan</sub> ]	7.08 - 10.59	8.47 $\pm$ 1.16	9.60	7.21 - 11.81	9.28 $\pm$ 1.81	7.41	6.75 - 9.15	7.79 $\pm$ 0.90	7.30
Anus to tip of snout length [D <sub>annus</sub> ]	40.98 - 45.88	43.32 $\pm$ 1.42	43.07	43.91 - 48.54	46.61 $\pm$ 1.71	48.54	43.99 - 48.75	46.27 $\pm$ 1.90	48.75
Body width at dorsal-fin origin [L <sub>corDo</sub> ]	16.16 - 19.10	18.09 $\pm$ 0.98	18.79	18.51 - 20.92	19.74 $\pm$ 1.02	20.01	17.26 - 22.15	20.07 $\pm$ 1.81	22.15
Body width at anal-fin origin [L <sub>corAn</sub> ]	12.09 - 14.80	13.55 $\pm$ 0.85	14.31	12.94 - 14.73	13.80 $\pm$ 0.72	14.45	11.31 - 14.57	13.03 $\pm$ 1.22	14.57
Body width at eighth postdorsal plate [l18]	8.59 - 11.83	10.28 $\pm$ 0.98	11.83	10.20 - 12.66	11.00 $\pm$ 0.91	12.66	9.63 - 11.94	10.72 $\pm$ 0.93	11.94
Body width at fourteenth postdorsal plate [l14]	4.41 - 7.01	5.22 $\pm$ 0.75	5.69	4.51 - 6.40	5.59 $\pm$ 0.70	6.40	3.72 - 5.28	4.72 $\pm$ 0.62	5.05
Body depth at dorsal-fin origin [H <sub>cor</sub> ]	10.21 - 13.87	11.92 $\pm$ 0.97	13.10	9.48 - 11.74	10.34 $\pm$ 0.83	10.83	12.22 - 13.46	12.69 $\pm$ 0.54	13.04
Minimum caudal peduncle depth [H <sub>minPC</sub> ]	3.05 - 3.74	3.41 $\pm$ 0.21	3.68	3.97 - 4.57	4.21 $\pm$ 0.21	4.57	3.20 - 3.72	3.46 $\pm$ 0.18	3.72
Head length (HL)	6.14 - 9.40	8.25 $\pm$ 1.17	9.40	6.50 - 7.96	7.42 $\pm$ 0.50	7.45	5.94 - 9.02	7.19 $\pm$ 1.33	9.02
Percents of HL									
Snout length [L <sub>mus</sub> ]	57.33 - 61.76	59.82 $\pm$ 1.26	59.26	56.49 - 60.87	58.30 $\pm$ 1.46	58.66	55.32 - 60.40	57.70 $\pm$ 2.32	55.32
Nostril to tip of snout length [L <sub>narBM</sub> ]	39.05 - 43.81	41.75 $\pm$ 1.44	40.85	40.13 - 43.61	41.56 $\pm$ 1.33	40.94	39.41 - 42.86	40.82 $\pm$ 1.44	40.69
Cleithral width [l <sub>ter</sub> ]	89.58 - 102.16	95.78 $\pm$ 4.04	97.55	94.16 - 105.67	99.93 $\pm$ 4.38	104.56	92.90 - 100.50	95.69 $\pm$ 3.14	96.90
Distal end of operculum to tip of snout length [OperBM]	77.85 - 84.32	81.60 $\pm$ 1.86	80.96	80.91 - 90.65	84.97 $\pm$ 3.46	86.71	80.17 - 86.73	82.71 $\pm$ 2.50	82.82
Maximum orbital diameter [D <sub>moil</sub> ]	16.01 - 18.77	17.28 $\pm$ 0.89	17.34	16.62 - 18.39	17.58 $\pm$ 0.63	18.39	17.07 - 20.12	18.78 $\pm$ 1.50	17.07
Interorbital width [D <sub>istintorb</sub> ]	32.65 - 38.04	36.06 $\pm$ 1.80	36.06	34.42 - 40.00	36.72 $\pm$ 2.15	40.00	36.20 - 41.02	38.20 $\pm$ 2.03	37.14
Head depth [H <sub>et</sub> ]	43.82 - 50.62	46.45 $\pm$ 1.87	46.60	41.58 - 46.85	43.40 $\pm$ 2.11	46.85	44.17 - 49.32	47.02 $\pm$ 1.86	46.78
Head depth at internostril [Hintnar]	31.68 - 43.93	36.74 $\pm$ 4.00	43.30	31.30 - 40.18	36.14 $\pm$ 3.75	37.85	34.32 - 36.30	35.03 $\pm$ 0.81	34.37
Meristic									
Number of premaxillary teeth [Nbdtissup]	33 - 46	37 $\pm$ 4	33	36 - 53	43 $\pm$ 6	53	44 - 59	51 $\pm$ 6	52
Number of dentary teeth [Nbdtisinf]	32 - 46	40 $\pm$ 5	32	35 - 51	40 $\pm$ 6	51	41 - 65	52 $\pm$ 9	56
Number of plates in the lateral series [Nblongit]	24 - 27	26 $\pm$ 1	26	24 - 25	25 $\pm$ 1	25	24 - 25	25 $\pm$ 0	24
Number of lateral abdominal plates [Nbdcutvent]	5 - 8	6 $\pm$ 1	6	5 - 7	6 $\pm$ 1	6	5 - 8	6 $\pm$ 1	5



Table I. - Continued.

	<i>Harttiella lucifer</i>			<i>Harttiella longicauda</i>			<i>Harttiella jannoli</i>		
	range	mean $\pm$ sd	holotype	range	mean $\pm$ sd	holotype	range	mean $\pm$ sd	holotype
N									
Standard length (SL)	30.99 - 42.68	36.87 $\pm$ 3.08	42.68	20.92 - 52.46	36.39 $\pm$ 8.26	52.46	22.78 - 47.13	36.88 $\pm$ 4.11	47.13
Percents of SL									
Head length [L <sub>het</sub> ]	21.81 - 25.49	23.54 $\pm$ 0.88	22.75	21.37 - 27.57	24.55 $\pm$ 1.34	21.37	22.66 - 30.06	25.54 $\pm$ 1.41	24.87
Predorsal length [L <sub>preDo</sub> ]	33.99 - 38.49	35.95 $\pm$ 1.19	35.29	33.07 - 40.57	36.58 $\pm$ 1.21	33.07	35.63 - 41.75	38.80 $\pm$ 1.17	36.73
Postdorsal length [L <sub>postDo</sub> ]	50.70 - 56.39	53.75 $\pm$ 1.51	53.37	50.47 - 57.85	53.89 $\pm$ 1.41	56.73	45.34 - 52.24	48.85 $\pm$ 1.33	46.96
Caudal peduncle length [L <sub>postAn</sub> ]	42.24 - 47.78	44.26 $\pm$ 1.48	46.65	39.07 - 49.48	43.61 $\pm$ 1.79	46.32	33.73 - 42.58	38.32 $\pm$ 1.54	39.23
Abdominal length [L <sub>abd</sub> ]	16.57 - 21.01	18.14 $\pm$ 0.92	17.95	12.46 - 21.00	18.40 $\pm$ 1.39	17.75	17.55 - 21.46	19.39 $\pm$ 0.91	19.07
Thoracic length [L <sub>thor</sub> ]	19.66 - 23.02	21.12 $\pm$ 1.06	22.35	15.85 - 21.40	18.43 $\pm$ 0.95	18.38	18.64 - 26.23	22.48 $\pm$ 1.62	23.32
Pectoral spine length [L <sub>pect</sub> ]	20.23 - 25.90	23.09 $\pm$ 1.36	24.79	18.92 - 25.91	21.87 $\pm$ 1.62	24.13	22.99 - 31.44	27.14 $\pm$ 1.54	29.00
Pelvic spine length [L <sub>pelv</sub> ]	18.76 - 23.16	21.23 $\pm$ 1.23	21.93	17.79 - 23.45	19.36 $\pm$ 1.17	19.63	21.02 - 31.70	24.67 $\pm$ 1.46	24.89
Dorsal spine length [L <sub>do</sub> ]	21.24 - 25.94	23.88 $\pm$ 1.26	25.94	18.83 - 25.07	21.39 $\pm$ 1.50	23.01	21.70 - 28.84	25.25 $\pm$ 1.61	24.34
Anal spine length [L <sub>an</sub> ]	11.97 - 18.15	16.13 $\pm$ 1.46	17.03	11.80 - 19.18	15.69 $\pm$ 1.43	15.65	15.16 - 25.32	17.77 $\pm$ 1.54	19.41
Anus to pelvic-fin origin length [D <sub>ampelv</sub> ]	9.12 - 11.27	10.13 $\pm$ 0.63	11.08	7.95 - 12.32	10.44 $\pm$ 0.92	11.32	9.57 - 15.38	12.88 $\pm$ 0.96	12.09
Anus to pectoral-fin origin length [D <sub>ampect</sub> ]	26.74 - 32.31	29.06 $\pm$ 1.57	31.65	23.18 - 30.80	28.46 $\pm$ 1.43	28.86	30.45 - 38.64	34.24 $\pm$ 1.67	35.77
Anus to anal-fin origin length [D <sub>anan</sub> ]	6.67 - 10.96	8.56 $\pm$ 1.17	7.76	6.44 - 12.91	8.33 $\pm$ 1.09	6.88	5.66 - 11.77	8.20 $\pm$ 1.14	8.47
Anus to tip of snout length [D <sub>annus</sub> ]	41.78 - 46.67	44.23 $\pm$ 1.37	46.51	40.05 - 47.92	44.94 $\pm$ 1.66	42.60	46.21 - 52.97	49.81 $\pm$ 1.63	49.61
Body width at dorsal-fin origin [L <sub>corDo</sub> ]	17.04 - 21.61	19.01 $\pm$ 1.00	18.13	13.95 - 20.17	17.28 $\pm$ 1.11	16.72	20.59 - 25.77	23.46 $\pm$ 1.18	21.77
Body width at anal-fin origin [L <sub>corAn</sub> ]	12.22 - 14.01	13.13 $\pm$ 0.48	13.66	9.66 - 13.84	11.99 $\pm$ 0.92	13.84	13.26 - 16.91	14.79 $\pm$ 0.78	15.85
Body width at eighth postdorsal plate [l14]	8.07 - 11.66	10.39 $\pm$ 0.83	10.78	6.37 - 11.61	9.29 $\pm$ 1.07	11.61	9.10 - 12.91	11.43 $\pm$ 0.72	12.33
Body width at fourteenth postdorsal plate [l14]	3.69 - 5.90	4.95 $\pm$ 0.55	5.08	2.61 - 4.88	3.99 $\pm$ 0.51	4.88	3.95 - 6.54	5.06 $\pm$ 0.50	5.37
Body depth at dorsal-fin origin [H <sub>cor</sub> ]	9.62 - 12.72	10.66 $\pm$ 0.87	10.07	8.17 - 11.57	9.86 $\pm$ 0.79	11.08	12.02 - 17.70	14.80 $\pm$ 1.14	15.38
Minimum caudal peduncle depth [H <sub>minPC</sub> ]	2.82 - 3.55	3.24 $\pm$ 0.21	3.30	1.96 - 2.96	2.53 $\pm$ 0.18	2.88	3.97 - 5.26	4.58 $\pm$ 0.35	4.73
Head length (HL)	7.72 - 9.71	8.66 $\pm$ 0.57	9.71	5.30 - 11.44	8.86 $\pm$ 1.74	11.21	6.64 - 11.72	9.38 $\pm$ 0.79	11.72
Percents of HL									
Snout length [L <sub>mus</sub> ]	55.21 - 60.30	58.21 $\pm$ 1.36	59.01	54.33 - 65.04	59.05 $\pm$ 2.39	56.82	53.64 - 66.74	60.05 $\pm$ 2.79	55.20
Nostril to tip of snout length [L <sub>narBM</sub> ]	38.19 - 43.92	40.93 $\pm$ 1.38	39.13	34.84 - 46.74	42.62 $\pm$ 2.27	40.32	37.29 - 52.65	41.60 $\pm$ 2.55	38.40
Cleithral width [l <sub>het</sub> ]	93.92 - 107.59	101.65 $\pm$ 3.28	103.71	88.25 - 107.89	94.50 $\pm$ 4.00	104.91	92.86 - 115.27	104.83 $\pm$ 5.24	105.12
Distal end of operculum to tip of snout length [O <sub>percBM</sub> ]	79.87 - 85.71	83.31 $\pm$ 1.66	83.93	77.50 - 100.37	84.86 $\pm$ 3.74	81.71	77.70 - 97.41	85.63 $\pm$ 4.19	84.90
Maximum orbital diameter [D <sub>moil</sub> ]	14.77 - 18.07	16.64 $\pm$ 0.75	16.58	15.57 - 25.51	18.49 $\pm$ 2.19	17.31	14.59 - 19.30	16.64 $\pm$ 1.02	14.59
Interorbital width [D <sub>istintorb</sub> ]	32.12 - 37.24	35.25 $\pm$ 1.21	36.35	29.74 - 40.74	33.82 $\pm$ 2.03	34.52	32.81 - 43.94	36.04 $\pm$ 1.88	33.11
Head depth [H <sub>het</sub> ]	40.20 - 46.97	44.16 $\pm$ 2.01	46.04	37.50 - 48.24	42.51 $\pm$ 2.62	44.96	41.60 - 58.50	49.79 $\pm$ 3.15	52.05
Head depth at internostril [H <sub>intnar</sub> ]	30.99 - 43.17	35.34 $\pm$ 2.28	33.68	27.99 - 36.53	32.19 $\pm$ 1.76	34.17	29.89 - 41.46	34.98 $\pm$ 2.79	35.67
Meristic									
Number of premaxillary teeth [N <sub>bdtsup</sub> ]	25 - 63	46 $\pm$ 9	55	21 - 43	32 $\pm$ 5	25	23 - 40	31 $\pm$ 4	27
Number of dentary teeth [N <sub>bdtsinf</sub> ]	28 - 67	47 $\pm$ 10	52	23 - 41	30 $\pm$ 4	23	21 - 44	31 $\pm$ 5	28
Number of plates in the lateral series [N <sub>blongit</sub> ]	25 - 27	26 $\pm$ 1	25	25 - 27	26 $\pm$ 1	26	23 - 26	25 $\pm$ 1	24
Number of lateral abdominal plates [N <sub>bscutvent</sub> ]	4 - 8	6 $\pm$ 1	5	5 - 8	6 $\pm$ 1	5	5 - 8	7 $\pm$ 1	7

Table I. - Continued.

	<i>Harttia guianensis</i>				<i>Harttia surinamensis</i>				<i>Harttia fluminensis</i>			
	range	mean $\pm$ sd	holotype	N	range	mean $\pm$ sd	holotype	67	range	mean $\pm$ sd	holotype	24
Standard length (SL)	25.20 - 167.00	92.62 $\pm$ 31.10	152.36		25.53 - 188.30	104.70 $\pm$ 39.54	188.30		67.64 - 151.14	119.06 $\pm$ 27.54	151.14	
Percents of SL												
Head length [L <sub>het</sub> ]	20.72 - 26.63	23.19 $\pm$ 1.33	21.03		22.63 - 29.61	24.15 $\pm$ 1.38	23.58		22.39 - 24.44	23.30 $\pm$ 0.61	23.03	
Predorsal length [L <sub>preDo</sub> ]	29.48 - 35.66	32.10 $\pm$ 1.05	31.86		31.65 - 38.74	33.01 $\pm$ 1.11	33.30		31.48 - 33.93	32.74 $\pm$ 0.61	33.12	
Postdorsal length [L <sub>postDo</sub> ]	53.13 - 60.75	57.35 $\pm$ 1.26	58.54		51.74 - 59.98	56.89 $\pm$ 1.36	55.92		54.19 - 58.18	56.63 $\pm$ 0.94	55.04	
Caudal peduncle length [L <sub>postAn</sub> ]	45.55 - 52.12	48.73 $\pm$ 1.29	49.09		45.01 - 49.39	47.67 $\pm$ 1.04	45.78		44.97 - 49.87	47.11 $\pm$ 1.05	44.97	
Abdominal length [L <sub>abd</sub> ]	14.88 - 19.87	17.71 $\pm$ 1.03	19.34		14.44 - 19.23	17.51 $\pm$ 1.01	18.41		17.09 - 19.99	18.52 $\pm$ 0.71	18.94	
Thoracic length [L <sub>thor</sub> ]	14.80 - 19.45	17.30 $\pm$ 0.91	17.53		15.85 - 21.90	17.73 $\pm$ 0.95	17.55		15.72 - 18.56	17.57 $\pm$ 0.75	18.07	
Pectoral spine length [L <sub>pect</sub> ]	18.88 - 29.22	23.14 $\pm$ 2.35	24.21		20.08 - 30.05	23.36 $\pm$ 2.08	28.20		21.41 - 28.33	24.82 $\pm$ 1.86	25.02	
Pelvic spine length [L <sub>pelv</sub> ]	16.34 - 20.63	18.69 $\pm$ 0.91	18.46		17.31 - 19.73	18.40 $\pm$ 0.56	18.16		17.99 - 19.95	18.84 $\pm$ 0.55	19.01	
Dorsal spine length [L <sub>do</sub> ]	19.29 - 25.07	22.60 $\pm$ 1.21	21.91		21.35 - 27.23	25.14 $\pm$ 1.24	25.39		23.24 - 27.69	25.01 $\pm$ 0.98	23.24	
Anal spine length [L <sub>an</sub> ]	10.83 - 14.29	12.56 $\pm$ 0.72	12.73		11.02 - 13.81	12.43 $\pm$ 0.66	11.74		12.14 - 14.10	13.16 $\pm$ 0.58	13.29	
Anus to pelvic-fin origin length [D <sub>ampelv</sub> ]	6.59 - 12.40	10.54 $\pm$ 0.91	12.40		7.21 - 11.72	10.63 $\pm$ 0.81	11.38		10.32 - 12.16	11.28 $\pm$ 0.47	11.93	
Anus to pectoral-fin origin length [D <sub>ampect</sub> ]	22.63 - 28.22	25.83 $\pm$ 1.15	28.22		24.26 - 27.80	26.10 $\pm$ 0.73	26.67		24.93 - 28.07	26.64 $\pm$ 0.77	27.12	
Anus to anal-fin origin length [D <sub>anan</sub> ]	7.44 - 10.15	8.86 $\pm$ 0.54	8.11		6.58 - 9.40	8.38 $\pm$ 0.53	8.89		7.94 - 10.00	8.90 $\pm$ 0.56	9.07	
Anus to tip of snout length [D <sub>annus</sub> ]	37.16 - 42.41	39.60 $\pm$ 1.15	40.82		38.92 - 45.16	40.91 $\pm$ 1.21	40.18		39.61 - 41.86	40.74 $\pm$ 0.70	41.60	
Body width at dorsal-fin origin [L <sub>corDo</sub> ]	12.30 - 21.51	18.27 $\pm$ 1.45	20.64		16.02 - 20.87	18.79 $\pm$ 1.07	20.55		17.24 - 21.66	19.54 $\pm$ 1.14	21.66	
Body width at anal-fin origin [L <sub>corAn</sub> ]	9.13 - 17.66	14.65 $\pm$ 1.39	17.66		9.87 - 17.16	14.93 $\pm$ 1.32	16.14		13.79 - 18.10	16.16 $\pm$ 1.01	18.10	
Body width at eighth postdorsal plate [l18]	8.33 - 14.83	11.82 $\pm$ 1.25	14.83		5.52 - 14.46	12.35 $\pm$ 1.63	14.13		11.28 - 14.94	13.52 $\pm$ 0.99	14.12	
Body width at fourteenth postdorsal plate [l14]	3.17 - 6.38	4.89 $\pm$ 0.60	6.16		3.60 - 6.88	5.45 $\pm$ 0.83	6.48		4.83 - 6.93	5.97 $\pm$ 0.64	5.77	
Body depth at dorsal-fin origin [H <sub>cor</sub> ]	6.98 - 10.13	8.25 $\pm$ 0.83	9.10		6.74 - 9.93	8.82 $\pm$ 0.61	8.71		8.75 - 10.23	9.45 $\pm$ 0.37	10.23	
Minimum caudal peduncle depth [H <sub>minPC</sub> ]	1.14 - 1.71	1.35 $\pm$ 0.11	1.50		1.25 - 1.86	1.44 $\pm$ 0.11	1.59		1.40 - 1.81	1.60 $\pm$ 0.11	1.81	
Head length (HL)	6.50 - 37.70	21.17 $\pm$ 6.36	32.04		7.56 - 44.40	24.87 $\pm$ 8.72	44.40		16.00 - 34.86	27.64 $\pm$ 6.05	34.80	
Percents of HL												
Snout length [L <sub>mus</sub> ]	44.62 - 58.04	54.51 $\pm$ 2.03	58.68		51.70 - 61.62	57.02 $\pm$ 2.13	59.91		55.25 - 81.68	58.89 $\pm$ 5.12	59.02	
Nostril to tip of snout length [L <sub>narBM</sub> ]	32.31 - 45.04	41.04 $\pm$ 1.85	45.69		40.21 - 47.97	43.71 $\pm$ 1.55	45.50		23.77 - 46.39	42.62 $\pm$ 4.27	44.43	
Cleithral width [l <sub>het</sub> ]	69.23 - 110.77	94.10 $\pm$ 7.87	110.49		76.06 - 103.94	91.84 $\pm$ 5.80	101.13		87.62 - 104.40	96.38 $\pm$ 4.37	104.40	
Distal end of operculum to tip of snout length [O <sub>percBM</sub> ]	66.15 - 83.27	78.51 $\pm$ 2.47	83.61		72.62 - 84.55	80.54 $\pm$ 2.37	81.08		79.53 - 84.43	81.99 $\pm$ 1.32	83.88	
Maximum orbital diameter [D <sub>moel</sub> ]	19.63 - 25.26	23.37 $\pm$ 1.08	22.22		19.11 - 26.67	22.71 $\pm$ 1.49	20.72		20.73 - 25.69	22.68 $\pm$ 1.43	23.56	
Interorbital width [D <sub>istintorb</sub> ]	19.54 - 26.26	22.04 $\pm$ 1.27	26.03		19.99 - 25.16	22.58 $\pm$ 1.07	23.87		21.88 - 26.18	24.25 $\pm$ 1.02	26.18	
Head depth [H <sub>het</sub> ]	29.31 - 41.79	35.27 $\pm$ 2.23	41.92		23.41 - 41.45	37.19 $\pm$ 2.47	34.01		37.31 - 43.30	38.94 $\pm$ 1.42	43.30	
Head depth at internostil [H <sub>intnar</sub> ]	23.15 - 33.95	27.61 $\pm$ 2.19	31.99		20.77 - 34.70	28.77 $\pm$ 2.52	29.73		28.01 - 36.93	31.14 $\pm$ 2.52	36.93	
Meristic												
Number of premaxillary teeth [N <sub>bdtsup</sub> ]	15 - 103	76 $\pm$ 14	88		10 - 113	78 $\pm$ 19	105		63 - 113	93 $\pm$ 13	99	
Number of dentary teeth [N <sub>bdtsinf</sub> ]	18 - 104	75 $\pm$ 15	97		29 - 116	77 $\pm$ 16	88		64 - 115	94 $\pm$ 14	105	
Number of plates in the lateral series [N <sub>blongit</sub> ]	27 - 31	29 $\pm$ 1	30		27 - 30	29 $\pm$ 1	27		29 - 30	29 $\pm$ 0	29	
Number of lateral abdominal plates [N <sub>bscutvent</sub> ]	0 - 9	7 $\pm$ 1	9		0 - 11	8 $\pm$ 2	8		6 - 9	7 $\pm$ 1	7	

Table I. - End.

	Harttia tuna			Harttia fowleri		
	range	mean ± sd	holotype	range	mean ± sd	holotype
N						
Standard length (SL)	36.93 - 172.21	117.43 ± 33.17	170.95	39.17 - 221.64	140.89 ± 49.13	143.92
Percents of SL						
Head length [Ltet]	23.52 - 28.29	24.97 ± 1.14	25.46	22.07 - 27.09	23.45 ± 0.95	23.52
Predorsal length [LpreDo]	31.86 - 35.40	33.58 ± 0.84	35.40	30.85 - 34.83	32.49 ± 0.91	32.78
Postdorsal length [LpostDo]	53.14 - 57.28	55.44 ± 1.10	53.77	54.04 - 59.36	57.19 ± 1.25	56.81
Caudal peduncle length [LpostAn]	44.04 - 48.66	46.54 ± 1.17	44.04	44.96 - 50.73	47.66 ± 1.29	46.79
Abdominal length [Labd]	14.09 - 20.66	18.34 ± 1.29	20.00	15.54 - 19.91	17.91 ± 1.18	19.03
Thoracic length [Lthor]	16.31 - 20.39	17.63 ± 0.80	16.82	16.63 - 19.57	18.20 ± 0.84	17.26
Pectoral spine length [Lpect]	19.80 - 27.37	23.13 ± 1.94	27.37	19.24 - 37.23	27.99 ± 4.22	21.75
Pelvic spine length [Lpelv]	16.49 - 19.03	17.96 ± 0.66	18.97	17.55 - 28.70	20.18 ± 2.30	17.55
Dorsal spine length [Ldo]	20.10 - 24.50	23.05 ± 1.21	23.30	20.00 - 28.15	24.98 ± 1.78	22.37
Anal spine length [Lan]	10.53 - 14.70	12.37 ± 0.83	14.70	11.90 - 16.79	14.28 ± 1.27	12.15
Anus to pelvic-fin origin length [Danpelv]	9.02 - 12.87	11.10 ± 0.84	12.87	8.04 - 12.01	11.02 ± 0.98	11.42
Anus to pectoral-fin origin length [Danpect]	24.08 - 27.89	26.39 ± 1.01	27.50	24.74 - 29.22	27.32 ± 1.23	27.11
Anus to anal-fin origin length [Danan]	6.72 - 9.85	8.76 ± 0.59	9.09	7.44 - 9.37	8.52 ± 0.46	8.55
Anus to tip of snout length [Danmus]	40.28 - 44.11	41.84 ± 1.02	43.43	38.70 - 43.11	41.24 ± 1.02	40.36
Body width at dorsal-fin origin [LcorDo]	14.76 - 21.79	19.58 ± 1.62	21.57	16.13 - 21.78	18.92 ± 1.22	19.29
Body width at anal-fin origin [LcorAn]	11.21 - 17.31	15.65 ± 1.47	17.16	11.18 - 16.36	14.56 ± 1.45	16.10
Body width at eighth postdorsal plate [l14]	9.07 - 14.90	13.28 ± 1.47	14.90	7.89 - 14.61	11.69 ± 1.32	14.61
Body width at fourteenth postdorsal plate [l14]	3.49 - 7.49	5.80 ± 0.89	6.30	3.27 - 6.69	5.01 ± 0.60	6.69
Body depth at dorsal-fin origin [Hcor]	7.79 - 9.73	8.64 ± 0.47	9.73	8.10 - 10.51	9.54 ± 0.67	8.20
Minimum caudal peduncle depth [HminPC]	1.26 - 1.80	1.43 ± 0.11	1.80	1.17 - 1.59	1.35 ± 0.13	1.38
Head length (HL)	10.42 - 43.52	29.10 ± 8.05	43.52	10.08 - 49.92	32.78 ± 11.16	32.90
Percents of HL						
Snout length [Lmus]	52.11 - 61.03	58.16 ± 2.16	60.89	52.18 - 61.03	56.52 ± 2.01	61.03
Nostril to tip of snout length [LnarBM]	38.68 - 45.88	43.94 ± 1.69	44.58	35.62 - 47.16	42.42 ± 2.21	44.83
Cleithral width [ltet]	72.74 - 102.55	93.29 ± 6.51	101.24	79.96 - 105.49	95.23 ± 5.96	95.41
Distal end of operculum to tip of snout length [OpercBM]	76.98 - 84.44	81.12 ± 1.66	82.86	74.67 - 84.58	79.68 ± 2.24	82.94
Maximum orbital diameter [Dmoel]	18.37 - 23.97	20.97 ± 1.12	19.12	20.04 - 27.28	23.04 ± 1.65	21.27
Interorbital width [Distinctorb]	21.09 - 25.67	23.12 ± 1.11	25.67	19.95 - 25.10	22.10 ± 1.24	23.15
Head depth [Htet]	31.96 - 38.77	36.52 ± 1.80	38.07	29.91 - 42.78	39.75 ± 2.37	37.79
Head depth at internostril [Hintnar]	24.66 - 33.47	28.66 ± 1.93	31.07	27.23 - 36.02	31.13 ± 1.99	28.70
Meristic						
Number of premaxillary teeth [Nbdtsup]	45 - 131	91 ± 19	131	45 - 100	79 ± 12	74
Number of dentary teeth [Nbdtsinf]	40 - 129	91 ± 19	129	40 - 83	69 ± 9	65
Number of plates in the lateral series [Nblongit]	29 - 30	29 ± 0	30	29 - 30	29 ± 0	30
Number of lateral abdominal plates [Nbscutvent]	5 - 9	7 ± 1	9	6 - 13	10 ± 2	10

Holm (1979) correction for multiple testing is applied for *a posteriori* tests. Pairwise Mantel correlations of the rank-transformed distances between matrices can also be computed to estimate the strength of the link between each pair of matrices. The CADM test was computed using 9,999 permutations of the three distances matrices. Prior to its computation, Euclidian distances were estimated from the mean populational scores of the two PCAs.

MCOA identifies the common structure in all data sets by providing a consensual typology (the compromise) maximizing the link with all tables simultaneously. This link is

expressed by the sum of squared covariances between the linear combinations of the variables of each table and the compromise.

Subsequently, in order to interpret the results provided by the MCOA from an evolutionary perspective, MCOA axes and associated variables were submitted to a test of phylogenetic autocorrelation (Abouheif, 1999; Pavoine *et al.*, 2008). This test is equivalent to a Moran's I (Moran, 1950) test of autocorrelation and was designed to detect similarities among adjacent observations in quantitative traits. The test was computed using the adephylo 1.1-0 package (Jom-



bart *et al.*, 2010) in R using 9,999 random permutations. A control for false discovery rate for multiple testing under dependency (Benjamini and Yekutieli, 2001) was applied since all tested variables may be proved to be phylogenetically dependent. The phylogenetic tree used for comparison was obtained from a study currently in progress (Covain *et al.*, 2009a; 2009b; 2009c). The tree topology was computed using probabilistic methods on a partitioned data set mixing mitochondrial and nuclear information. The COI marker was not used for this study, providing therefore a relatively independent observation.

## RESULTS

### Morphometric analysis of all populations and species of Guianese Harttiini

Morphological data were mainly structured on the first two axes of PCA (Fig. 1C) that accounted for 70.34% of the total variation (53.02% for axis 1 and 17.32% for axis 2). The first axis split the Harttiini into three groups (Fig. 1A) corresponding to *Harttiella* representatives on the negative side, followed by representatives of *Harttia*, and finally representatives of the former *Cteniloricaria* except *H. fowleri*. The second axis split *Harttia* representatives on the negative side, from *Harttiella* and the former *Cteniloricaria* representatives. Three morphological groups were consequently recognised and named: *Cteniloricaria*, *Harttia*, and *Harttiella* groups. On the positive side of axis 1, the *Cteniloricaria* group corresponded to high values for maximum orbital diameter, number of plates in the lateral series, caudal peduncle length, and postdorsal length (Fig. 1B). It consisted of representatives of the type species of the genus *C. platystoma*, different populations of *H. maculata* (Corantijn, Suriname, Maroni, and Mana Rivers) and a population from Paru de Oeste River. On the second axis, the *Harttia* group was characterized by high negative values for the number of dentary teeth, number of premaxillary teeth, body width at eighth postdorsal plate, body width at anal-fin origin, and body width at fourteenth postdorsal plate (Fig. 1B). The *Harttia* group comprised representatives of *H. guianensis* (Maroni, Sinnamary, and Approuague Rivers), *H. surinamensis*, *H. fowleri*, and the populations from Coppename and Paru de Oeste rivers. The *Harttiella* group, located on the negative side of the first axis, corresponded to high values for predorsal length, minimum caudal peduncle depth, anus to pectoral-fin origin length, cleithral width, interorbital width, head depth at internostril, head depth, snout length, thoracic length, distal end of operculum to tip of snout length, pelvic spine length, body width at dorsal-fin origin, body depth at dorsal-fin origin, anus to tip of snout length, anus to pelvic-fin origin length, head length, nostril to tip of snout length, and abdominal length (Fig. 1B). The *Harttiella*

group comprised the type species of the genus, *H. crassicauda* from Nassau Mountain in Suriname, and several populations from French Guiana (Kotika Mountain, Trinité Mountains, Crique Grillon, Crique Aya, Crique Cascade, Crique Coeur Maroni, Crique Limonade, Atachi Bakka Mountains, and Lucifer Mountains). Two morphological tendencies were highlighted by the analysis, with a sub-group made up of *H. crassicauda* plus the populations from Kotika, Atachi Bakka and Trinité Mountains, and the other containing all other populations. The first group corresponded to stockier forms of the genus, whereas the second group assembled slender representatives.

### DNA barcode analysis of Guianese Harttiini

The sequence alignment of the 42 barcodes reached a total length of 594 positions including a single ambiguity (Y in position 81 of the COI sequence of *C. maculata* from Suriname River). No insertions, deletions, or stop codons were observed in any sequence. The global base composition was: A = 0.242, T = 0.290, G = 0.180, and C = 0.288. The  $\chi^2$  test of heterogeneity of nucleotide frequencies among OTUs failed to reject the null hypothesis ( $\chi^2 = 18.44$ , p-value = 1) implying that the data set is not at base composition equilibrium. A slight tendency toward AT enrichment was present in the data since the GC content per sequence (Tab. II) was always below 0.5 (mean =  $0.468 \pm 0.012$ ). In first codon position (GC1) the GC content reached a mean value of  $0.538 \pm 0.009$ , vs  $0.440 \pm 0.00077$  in second position (GC2), and  $0.426 \pm 0.034$  in third position (GC3). The maximum in GC content was thus observed in first position, with a mean value above 0.5, whereas a minimum was reached in third position with a significant enrichment in AT bases (0.574). The test on the Index of substitution saturation (Iss) resulted in Iss significantly smaller than Iss.c assuming both a symmetrical and an asymmetrical topology, implying little saturation in the data. The NJ tree reconstruction computed with the K2P distance matrix grouped the different species and populations within three clusters corresponding to the *Harttiella*, *Cteniloricaria*, and *Harttia* groups as previously defined with exception of *H. fowleri* that formed the root of the tree (Fig. 2A). These three groups possessed very strong statistical support (100% bootstraps). Within the *Harttiella* group the total amount of K2P corrected distances varied from 0 to 0.12. In the NJ tree, the first diverging populations comprised representatives from Mana River (Lucifer Mountains and Crique Cascade) and Maroni River (Crique Limonade), a grouping statistically strongly supported (100% bootstrap). These two populations were genetically almost identical with null K2P distances within-population and a between-population distance of 0.0017. The second well-supported (100% bootstrap) diverging group comprised representatives from Approuague River (Crique Cascades), Mana River (Crique Aya), and Sinnamary River

(Trinité Mountains). Within-population variation ranged from 0 to 0.003, whereas between-population distances ranged between 0.0017 and 0.005. The last group, also statistically well supported (72.3% bootstrap) comprised populations from Maroni River (Atachi Bakka Mountains and Nassau Mountains) including the type species *H. crassicauda*, and from Orapu River (Crique Grillon). The within-population variations ranged from 0 to 0.0017 whereas between-population variations were comprised between 0.031 and 0.034. The *Harttia* group included all populations of *H. guianensis* (Approuague, Sinnamary, and Maroni Rivers), *H. surinamensis* (Suriname River), and the populations from Coppename and Paru de Oeste Rivers. Within the *H. guianensis* lineage, the K2P distances ranged from 0 to 0.0017, and with other *Harttia*, it diverged by K2P distances ranging from 0.064 (*H. surinamensis*) to 0.077 (Paru de Oeste River). *H. surinamensis* diverged from other representatives by distances ranging from 0.012 (Coppename River) to 0.070 (Paru de Oeste River), while it differed by a mean distance of 0.065 with *H. guianensis*. The specimens from Coppename River diverged from other representatives by distances comprised between 0.012 (*H. surinamensis*) and 0.068 (Paru de Oeste River). The population from the Paru de Oeste possessed the strongest divergence compared to other representatives, ranging from 0.068 (Coppename River) to 0.077 (*H. guianensis* from Approuague River). The *Cteniloricaria* group comprised *C. platystoma* (type species), the different populations of *C. maculata* (Coran-

tijn, Suriname, Maroni and Mana Rivers), as well as an unnamed population from Paru de Oeste River. The latter possessed the strongest divergence from other populations with K2P distances comprised between 0.057 (*C. platystoma*, Essequibo River) and 0.070 (*C. maculata*, Mana River). *C. platystoma* connected within the different populations of *C. maculata* and differed from them by distances varying from 0.003 (Corantijn River) to 0.019 (Maroni River). The within-population variation in *C. maculata* ranged between 0.005 and 0.025. *H. fowleri* connected at the base of the tree, and possessed mean sequence divergences ranging from 0.149 with the *Cteniloricaria* group, and 0.182 and 0.208 in average with the *Harttia* and *Harttiella* groups respectively. In the light of this topology the GC content was explored for the different groups constituted (with exclusion of *H. fowleri*, alone in its own group). Significant differences in mean were recorded for the global GC content (Kruskal-Wallis test:  $\chi^2_{K-W} = 15.8207$ , p-value = 0.0004), the first position ( $\chi^2_{K-W} = 11.9222$ , p-value = 0.0026), and the third position ( $\chi^2_{K-W} = 18.6343$ , p-value < 0.0001), but no significant difference was highlighted for the second position ( $\chi^2_{K-W} = 5.8333$ , p-value = 0.0541). Concerning the global GC content, a significant difference was detected between *Harttia* and *Cteniloricaria* + *Harttiella* groups, with *Harttia* having a smaller GC content [mean =  $0.442 \pm 0.007$  vs  $0.470 \pm 0.004$  in *Cteniloricaria* (Wilcoxon test: W = 0, p-value = 0.0024) and  $0.472 \pm 0.003$  in *Harttiella* (W = 0, p-value < 0.0001)]. No significant difference was recorded

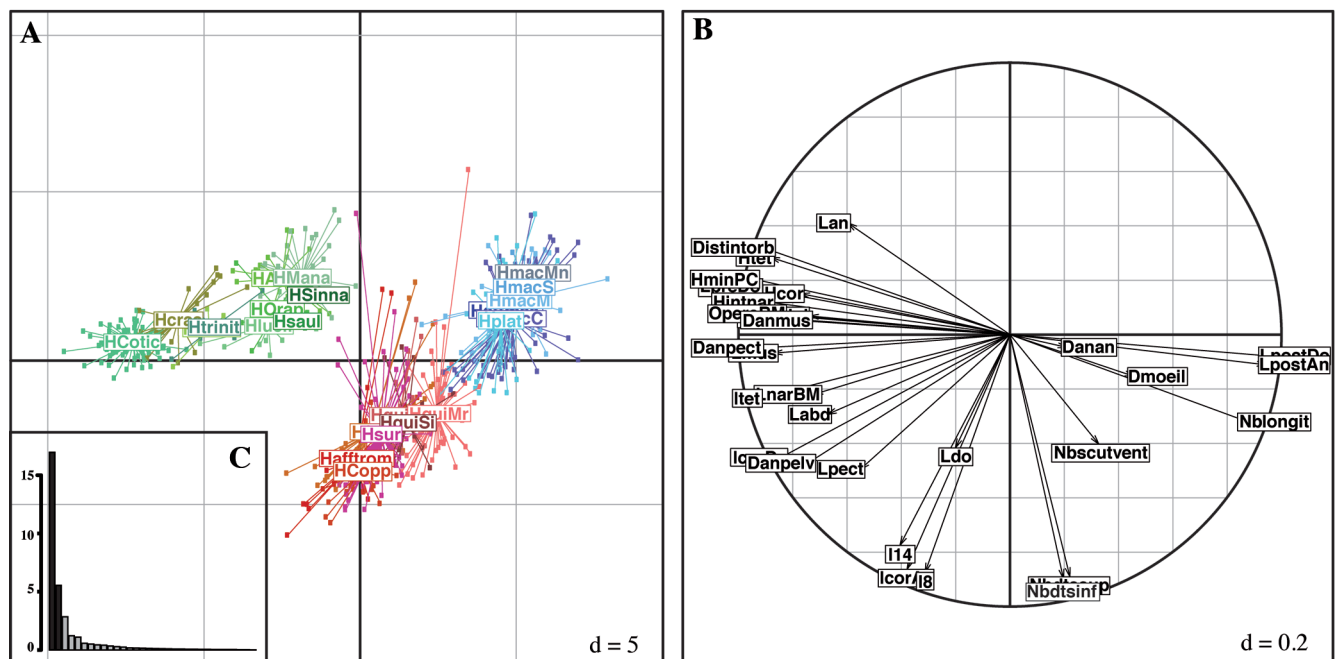


Figure 1. - Principal Components Analysis of the morphometric data table of Guianese Harttiini computed using the correlation matrix on log ratio transformed measurements and untransformed counts. **A:** Projection of the 618 individuals onto the first factorial plane of the PCA; populations and species labelled as in tables II and V, and the list of material. **B:** Correlation circle of the 32 morphometric variables labelled as in table I. Axis 1 horizontal, and axis 2 vertical. **C:** Eigenvalues.

between *Cteniloricaria* and *Harttiella* ( $W = 69$ ,  $p$ -value = 0.4351). In the first position, *Cteniloricaria* possessed a greater GC1 content (mean =  $0.548 \pm 0.008$ ) than *Harttia* [mean =  $0.530 \pm 0.003$  ( $W = 0$ ,  $p$ -value = 0.0017)] and *Hart-*

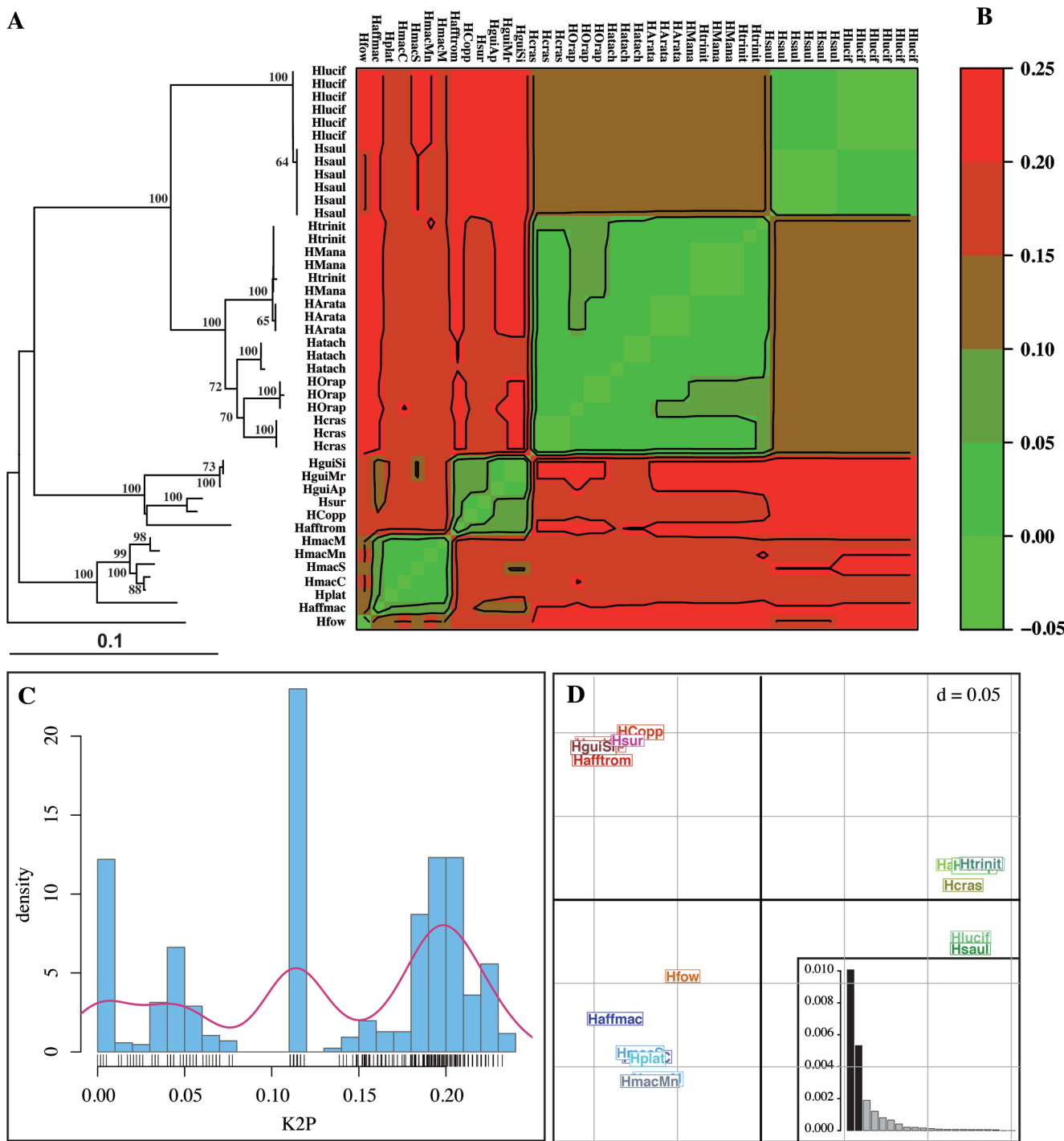


Figure 2. - Analysis of the 42 DNA barcodes of Guianese Harttiini. **A:** NJ tree reconstructed from the K2P distances matrix computed on 594 bases of the mitochondrial COI gene; numbers above branches indicate bootstrap support using 9,999 pseudoreplicates; scale indicates K2P distances; tips labelled as in table II and the list of material. **B:** Levelplot of the ordinated K2P matrix; scale indicates the levels of variation in K2P distances. **C:** Histogram of variation of the K2P distances using 861 pairwise comparisons; scale indicates the frequencies of pairwise comparisons in a definite range. **D:** Principal coordinates analysis of the K2P matrix; taxa labelled as in tables II and V, and the list of material.



Table II. - Taxa list, specimen and sequence data for the 42 Harttiini analysed in this study. Abbreviations of the different species and populations used in the analyses are provided between square brackets. The acronyms of institutions follow Fricke and Eschmeyer (2010).

Species	Catalog number	Field number	Locality	GenBank No.	GC content	GC1	GC2	GC3
<i>Harttia guianensis</i> [HguiMr]	MHNG 2643.016	GF00-351	French Guiana, Maroni River drainage, Marouini River	JF292266	0.448	0.535	0.440	0.370
<i>Harttia guianensis</i> [HguiSi]	MHNG 2680.053	RV-21	French Guiana, Sinnamary River drainage, Saut Takari Tanté	JF292267	0.448	0.535	0.440	0.370
<i>Harttia guianensis</i> [HguiAp]	MHNG 2662.091	GF03-160	French Guiana, Approuague River drainage, Crique Aratai	JF292265	0.447	0.535	0.440	0.365
<i>Harttia surinamensis</i> [Hsur]	MHNG 2674.042	SU05-001	Suriname, Suriname River drainage, Gran Rio	JF292264	0.438	0.525	0.440	0.350
<i>Harttia fluminensis</i> [HCopp]	MHNG 2690.013	SU01-445	Suriname, Coppename River drainage, Raleighvallen	JF292263	0.437	0.530	0.440	0.340
<i>Harttia tuna</i> [Haffrom]	MHNG 2704.029	SU07-644	Brazil, Paru de Oeste River drainage, Four Brothers	JF292262	0.433	0.520	0.435	0.345
<i>Harttia fowleri</i> [Hfow]	MHNG 2643.022	GF99-202	French Guiana, Oyapock River drainage, Crique Gabaret	JF292255	0.497	0.555	0.440	0.495
<i>Cteniloricaria platystoma</i> [Hplat]	MHNG 2650.082	GY04-336	Guyana, Essequibo River drainage, Siparuni River	JF292257	0.465	0.545	0.440	0.410
<i>Cteniloricaria platystoma</i> [HmacC]	MHNG 2672.067	SU05-340	Suriname, Corantijn River drainage, Wonotobo Falls	JF292258	0.465	0.545	0.440	0.410
<i>Cteniloricaria platystoma</i> [HmacS]	MHNG 2674.003	SU05-039	Suriname, Suriname River drainage, Awaradam	JF292259	0.472	0.545	0.440	0.433
<i>Cteniloricaria platystoma</i> [HmacM]	MHNG 2643.014	GF00-092	French Guiana, Maroni River drainage, Marouini River	JF292261	0.472	0.545	0.440	0.430
<i>Cteniloricaria platystoma</i> [HmacMn]	MHNG 2700.054	GF07-265	French Guiana, Mana River drainage, Crique Aya	JF292260	0.473	0.545	0.440	0.435
<i>Cteniloricaria napova</i> [Haffmac]	MHNG 2704.030	SU07-650	Brazil, Paru de Oeste River drainage, Four Brothers	JF292256	0.475	0.565	0.440	0.420
<i>Harttiella crassicauda</i> [Hcras]	MHNG 2674.051	MUS 221	Suriname, Marowijn River drainage, Nassau Mountains in Paramaka Creek	JF292268	0.478	0.530	0.440	0.465
<i>Harttiella crassicauda</i> [Hcras]	MHNG 2674.051	MUS 231	Suriname, Marowijn River drainage, Nassau Mountains in Paramaka Creek	JF292269	0.478	0.530	0.440	0.465
<i>Harttiella crassicauda</i> [Hcras]	MHNG 2679.098	MUS 306	Suriname, Marowijn River drainage, Nassau Mountains in Paramaka Creek	JF292270	0.478	0.530	0.440	0.465
<i>Harttiella pilosa</i> [HOrap]	MHNG 2724.002	GF03-033	French Guiana, Orapu River drainage, Tortue Mountains in Crique Grillon	JF292271	0.475	0.525	0.440	0.460
<i>Harttiella pilosa</i> [HOrap]	MHNG 2682.055	GF06-344	French Guiana, Orapu River drainage, Tortue Mountains in Crique Grillon	JF292272	0.473	0.525	0.440	0.455
<i>Harttiella pilosa</i> [HOrap]	MHNG 2682.055	GF06-343	French Guiana, Orapu River drainage, Tortue Mountains in Crique Grillon	JF292273	0.473	0.525	0.440	0.455
<i>Harttiella parva</i> [Hatach]	MHNG 2723.093	MUS 606	French Guiana, Maroni River drainage, Atachi Bakka Mountains	JF292274	0.468	0.530	0.440	0.435
<i>Harttiella parva</i> [Hatach]	MHNG 2723.093	MUS 607	French Guiana, Maroni River drainage, Atachi Bakka Mountains	JF292275	0.468	0.530	0.440	0.435
<i>Harttiella parva</i> [Hatach]	MHNG 2723.093	MUS 611	French Guiana, Maroni River drainage, Atachi Bakka Mountains	JF292276	0.468	0.530	0.440	0.435
<i>Harttiella intermedia</i> [Htrinit]	MHNG 2713.087	MUS 650	French Guiana, Sinnamary River drainage, Trinité Mountains in Crique Grand Leblond	JF292284	0.473	0.535	0.440	0.445
<i>Harttiella intermedia</i> [Htrinit]	MHNG 2713.087	MUS 651	French Guiana, Sinnamary River drainage, Trinité Mountains in Crique Grand Leblond	JF292285	0.475	0.535	0.440	0.450
<i>Harttiella intermedia</i> [Htrinit]	MHNG 2713.087	MUS 652	French Guiana, Sinnamary River drainage, Trinité Mountains in Crique Grand Leblond	JF292281	0.473	0.535	0.440	0.445
<i>Harttiella lucifer</i> [Hlucif]	MHNG 2721.088	GF10-034	French Guiana, Mana River drainage, Lucifer Mountains in Crique Cascade	JF292291	0.468	0.545	0.440	0.420
<i>Harttiella lucifer</i> [Hlucif]	MHNG 2721.088	GF10-043	French Guiana, Mana River drainage, Lucifer Mountains in Crique Cascade	JF292295	0.468	0.545	0.440	0.420

Table II. - Continued.

Species	Catalog number	Field number	Locality	GenBank No.	GC content	GC1	GC2	GC3
<i>Harttiella lucifer</i> [Hlucif]	MHNG 2721.088	GF10-037	French Guiana, Mana River drainage, Lucifer Mountains in Crique Cascade	JF292294	0.468	0.545	0.440	0.420
<i>Harttiella lucifer</i> [Hlucif]	MHNG 2721.091	GF10-051	French Guiana, Mana River drainage, Lucifer Mountains	JF292292	0.468	0.545	0.440	0.420
<i>Harttiella lucifer</i> [Hlucif]	MHNG 2721.091	GF10-053	French Guiana, Mana River drainage, Lucifer Mountains	JF292296	0.468	0.545	0.440	0.420
<i>Harttiella lucifer</i> [Hlucif]	MHNG 2721.091	GF10-055	French Guiana, Mana River drainage, Lucifer Mountains	JF292293	0.468	0.545	0.440	0.420
<i>Harttiella lucifer</i> [Hsaul]	MHNG 2712.085	MUS 592	French Guiana, Maroni River drainage, Crique Limonade	JF292290	0.470	0.545	0.440	0.425
<i>Harttiella lucifer</i> [Hsaul]	MHNG 2712.085	MUS 593	French Guiana, Maroni River drainage, Crique Limonade	JF292288	0.470	0.545	0.440	0.425
<i>Harttiella lucifer</i> [Hsaul]	MHNG 2712.085	MUS 591	French Guiana, Maroni River drainage, Crique Limonade	JF292289	0.470	0.545	0.440	0.425
<i>Harttiella lucifer</i> [Hsaul]	MHNG 2712.085	MUS 595	French Guiana, Maroni River drainage, Crique Limonade	JF292286	0.470	0.545	0.440	0.425
<i>Harttiella lucifer</i> [Hsaul]	MHNG 2712.085	MUS 596	French Guiana, Maroni River drainage, Crique Limonade	JF292287	0.470	0.545	0.440	0.425
<i>Harttiella longicauda</i> [HMana]	MHNG 2699.070	GF07-026	French Guiana, Mana River drainage, Crique Aya	JF292280	0.473	0.535	0.440	0.445
<i>Harttiella longicauda</i> [HMana]	MHNG 2699.070	GF07-082	French Guiana, Mana River drainage, Crique Aya	JF292283	0.473	0.535	0.440	0.445
<i>Harttiella longicauda</i> [HMana]	MHNG 2699.070	GF07-111	French Guiana, Mana River drainage, Crique Aya	JF292282	0.473	0.535	0.440	0.445
<i>Harttiella longicauda</i> [HArata]	MHNG 2723.094	MUS 456	French Guiana, Approuague River drainage, Crique Cascades	JF292279	0.475	0.535	0.440	0.450
<i>Harttiella longicauda</i> [HArata]	MHNG 2723.094	MUS 470	French Guiana, Approuague River drainage, Crique Cascades	JF292278	0.475	0.535	0.440	0.450
<i>Harttiella longicauda</i> [HArata]	MHNG 2723.094	MUS 463	French Guiana, Approuague River drainage, Crique Cascades	JF292277	0.475	0.535	0.440	0.450

*tiella* [mean =  $0.537 \pm 0.007$  ( $W = 146.5$ ,  $p$ -value = 0.003)], whereas no difference in GC1 was found between *Harttia* and *Harttiella* ( $W = 48$ ,  $p$ -value = 0.0789). In the third position, GC3 content was highly variable between groups with a significantly smaller GC3 in *Harttia* [mean =  $0.357 \pm 0.013$  vs  $0.423 \pm 0.011$  in *Cteniloricaria* ( $W = 0$ ,  $p$ -value = 0.0025), and  $0.439 \pm 0.016$  in *Harttiella* ( $W = 0$ ,  $p$ -value < 0.0001)]. Moreover, the GC3 content was significantly lower in *Cteniloricaria* than in *Harttiella* ( $W = 37.5$ ,  $p$ -value = 0.0153).

Assuming the ordination of the different species and populations reinforced by lineage-specific variations in GC contents, the matrix was reordinated and a levelplot reconstructed (Fig. 2B). Three levels of variation were recorded in the matrix corresponding to within species (between population), between species, and between genera levels. The within species level (light green) ranged from 0 to 0.026 (mean =  $0.003 \pm 0.005$ ). The between species within genera level (green to khaki to brown) ranged from 0.031 to 0.119 (mean =  $0.088 \pm 0.033$ ) and possessed the widest range of variation with 2 maxima (Fig. 2C). The first one was located at a mean value of  $0.047 \pm 0.011$ , and the second at  $0.113 \pm 0.002$ . The between genera level (dark red to light red) ranged from 0.139 to 0.232 (mean =  $0.197 \pm 0.019$ ).

The PCoA computed from the K2P distances matrix (Fig. 2D) splits the *Harttiini* along the two first axes that accounted for 71.24% of the total inertia. The first principal coordinate that explained 46.59% of the total inertia splits *Harttiella* in positive scores from *Harttia* and *Cteniloricaria* in negative scores. The second principal coordinate (24.64% of the total inertia) splits *Harttia* (positive scores) from *Cteniloricaria* (negative scores). The position of *H. fowleri*, close to *Cteniloricaria*, was in contradiction with the morphology that grouped it among *Harttia* representatives.

#### Analysis of the ecology and distribution of Guianese *Harttiini*

The PCA computed using the NIPALS revealed structures of the ecological and distributional data on the first axis (Fig. 3C) that explained 41.11% of the total variation. This axis splits the *Harttiini* into two groups (Fig. 3A) with representatives of *Harttiella* in negative values, and representatives of *Cteniloricaria* and *Harttia* gathered together rather in positive values. The single specimen of *Cteniloricaria* from Mana River drainage (Crique Aya) was grouped with representatives of *Harttiella* due to the fact that it was collected together with *Harttiella* representatives, and that it formed the unique known specimen from this drainage. Three variables were strongly correlated with the first axis (Fig. 3B): the altitude, the type of biotope and the temperature. High altitude, creek, and low temperature characterized *Harttiella*, which are inhabitants of small creeks in mountainous areas where the water is cooler, whereas *Harttia* and

*Cteniloricaria* are representative of the main stream of rivers, in lowlands, where the water is warmer.

### Multiple co-inertia analysis of morphology, genetics and ecology of Guianese Harttiini

The results obtained from the three previous analyses seemed to imply that a common structure was shared between the three types of information (morphology, genetics, and ecology), in particular considering the first axis. The three tables were consequently reduced to 19 common species and populations and submitted to preliminary analyses prior to the multi-table analysis. A first assessment of the relationships between morphology, genetics, and ecology was performed using the CADM test. Prior to its computation, mean population scores obtained from the PCA of the morphological and ecological data were converted into distances matrices using the canonical metrics. The K2P matrix was used as is. A first visual representation of the common structure present within each table was obtained by levelplots of the three distances matrices (Tab. III). The structure of the information was mainly organized into three blocs corresponding to the three groups previously defined (Tab. III, columns Genetic and Morphology). The ecological data set (Tab. III, column Ecology) was organized into two blocs corresponding to the splitting between *Harttiella* and *Harttia* + *Cteniloricaria* despite important background noise. The global CADM test showed a strong and significant correlation between all distance matrices ( $p$ -value = 0.0001;  $W = 0.666$ ). *A posteriori* tests did not detect any conflicting matrix, since each of them displayed significant correlations with respect to the other matrices (Tab. III). Pairwise Mantel correlations highlighted that the genetic data were more correlated to the morphometric (Mantel = 0.596,  $p$ -value = 0.0001) and ecological data (Mantel = 0.509,  $p$ -value = 0.0001) than were the latter to morphometric data (Mantel = 0.393,  $p$ -value = 0.0007). The first plane of MCOA accounted for 74.11% of the total co-structure (54.74% for axis 1 and 19.37% for axis 2) (Fig. 4C). MCOA statistics provided in table III showed that the amount of variation explained by MCOA axes is quite equivalent to those obtained in the separated analyses: 99.46% ( $((0.481 + 0.252)/(0.486 + 0.251) = 0.733/0.737)$ ) of the genetic data structure, 99.39% of the morphological data structure, and 93.05% of the ecological data structure were recovered by the first two axes. The contribution of each table to the quantity maximized by MCOA (i.e., sum of squared covariances between the linear combinations of the variables of each table and the compromise) is also presented ( $\text{Cov}^2$  in Tab. III). The associated correlations ( $\text{Cos}^2$  in Tab. III) showed that the first two axes of the compromise are strongly linked to each separated table except for the second axis of ecological data (0.957 and 0.953 for the genetic data, 0.922 and 0.908 for the morphometric data, and 0.868 and 0.324 for the ecological data). The first axis of MCOA

aligned the *Harttiella* group (negative scores) followed by *Harttia* then *Cteniloricaria* groups (positive scores). The second axis splits *Harttia* from *Cteniloricaria*, but poorly characterized *Harttiella*. The projection of genetic, morphological and ecological information onto MCOA axes (Fig. 4A) illustrate the most important differences between the three types of information (dots) and the compromise established by the MCOA (labels). These differences mainly concerned the second axis, and particularly the specimen of *C. maculata* from Crique Aya. The second unstable position between the three tables and the compromise concerned *H. fowleri*, which stayed distinct but close to *Harttia*. Correlations with MCOA axes (Fig. 4B) allow identification of the most important variables. On axis 1 these variables corresponded, in decreasing order of scores (absolute values for negative scores), to: the altitude, conductivity, longitude, interorbital width, minimum caudal-peduncle depth, predorsal length, head depth, head depth at internostril, anus to tip of snout length, anus to pectoral-fin origin length, thoracic length, pelvic-spine length, distal end of operculum to tip of snout length, body depth at dorsal-fin origin, snout length, head length, cleithral width, and latitude in negative values, and to the: first principal coordinate of PCoA, biotope, temperature, number of plates in the lateral series, postdorsal length, caudal-peduncle length, number of lateral abdominal plates, and maximum orbital diameter in positive values. On the second axis the variables with greater scores corresponded to the second principal coordinate of the PCoA in negative values, and in decreasing order to the: body width at anal-fin origin, body width at eighth postdorsal plate, number of dentary teeth, number of premaxillary teeth, and anus to pelvic-fin origin length in positive values (Tab. IV).

The Abouheif's tests identified a significant positive phylogenetic autocorrelation for the first two axes of MCOA ( $C\text{-mean}_1 = 0.8284$ ,  $p$ -value = 0.0001;  $C\text{-mean}_2 = 0.6907$ ,  $p$ -value = 0.0001). No significant phylogenetic dependence was recovered on other axes that were consequently discarded from further interpretation. Results of tests conducted on the different variables constituting the three initial tables are provided in table IV. As expected, axes of the PCoA describing the structure of the genetic data were found to be significantly positively autocorrelated with the phylogeny, and particularly axes 1 (A1) and 2 (A2) displaying the strongest scores (in absolute values) on axes 1 and 2 of the MCOA respectively. Twenty nine morphometric variables out of 32 were found to be significantly phylogenetically dependent. Only three variables: the dorsal-spine length, the pectoral-spine length, and the anus to anal-fin origin length displayed variations independent from the phylogeny. Concerning the ecological and distributional variables, two ecological variables (type of biotope and temperature), and two geographical variables (altitude and longitude) were found to be positively linked to the evolutionary history of Harttiini.



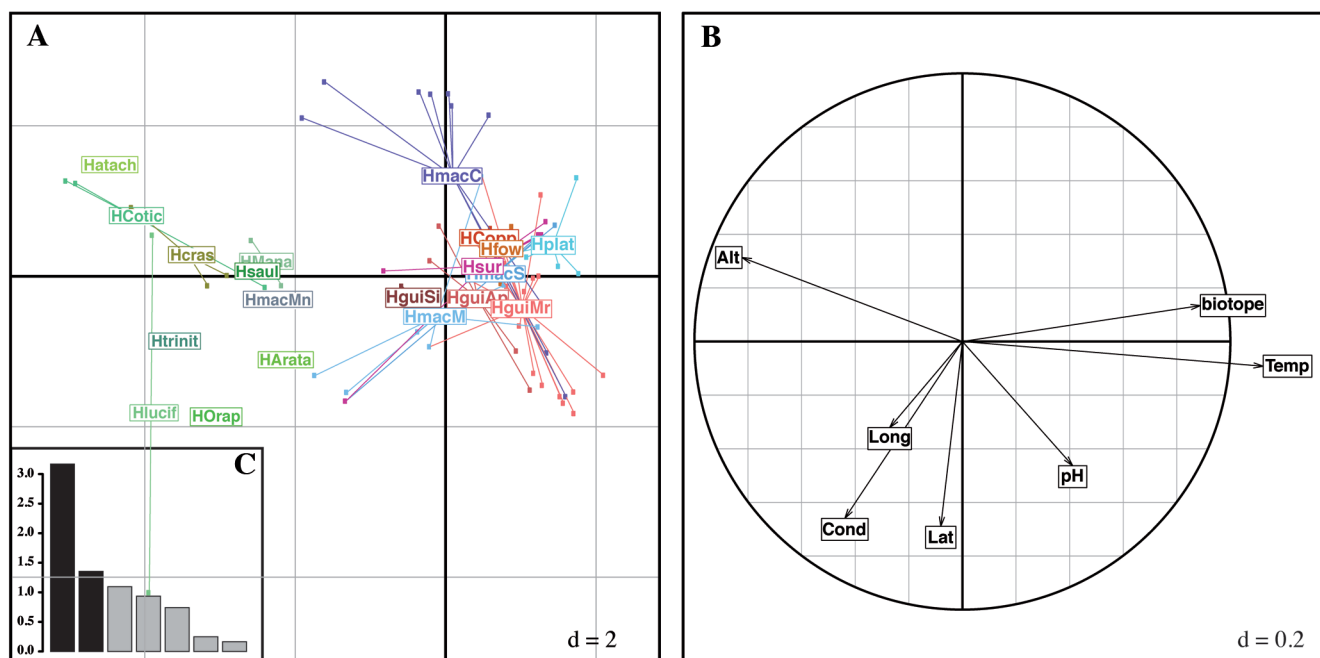


Figure 3. - Principal Components Analysis of the ecology-distribution data of Guianese Harttiini using the NIPALS algorithm for missing data. **A**: Projection of the 88 individuals onto the first factorial plane of the PCA; populations and species labelled as in tables II and V, and the list of material. **B**: Correlation circle of the 4 ecological and 3 distributional variables: biotope: type of biotope 1 = creek, 2 = river; Temp: temperature in degrees Celsius; pH: potential Hydrogen; Cond: conductivity in  $\mu\text{S}\cdot\text{cm}^{-1}$ ; Lat: latitude in decimal degrees; Long: longitude in decimal degrees; Alt: altitude in meters above sea level. Axis 1 horizontal, and axis 2 vertical. **C**: Eigenvalues.

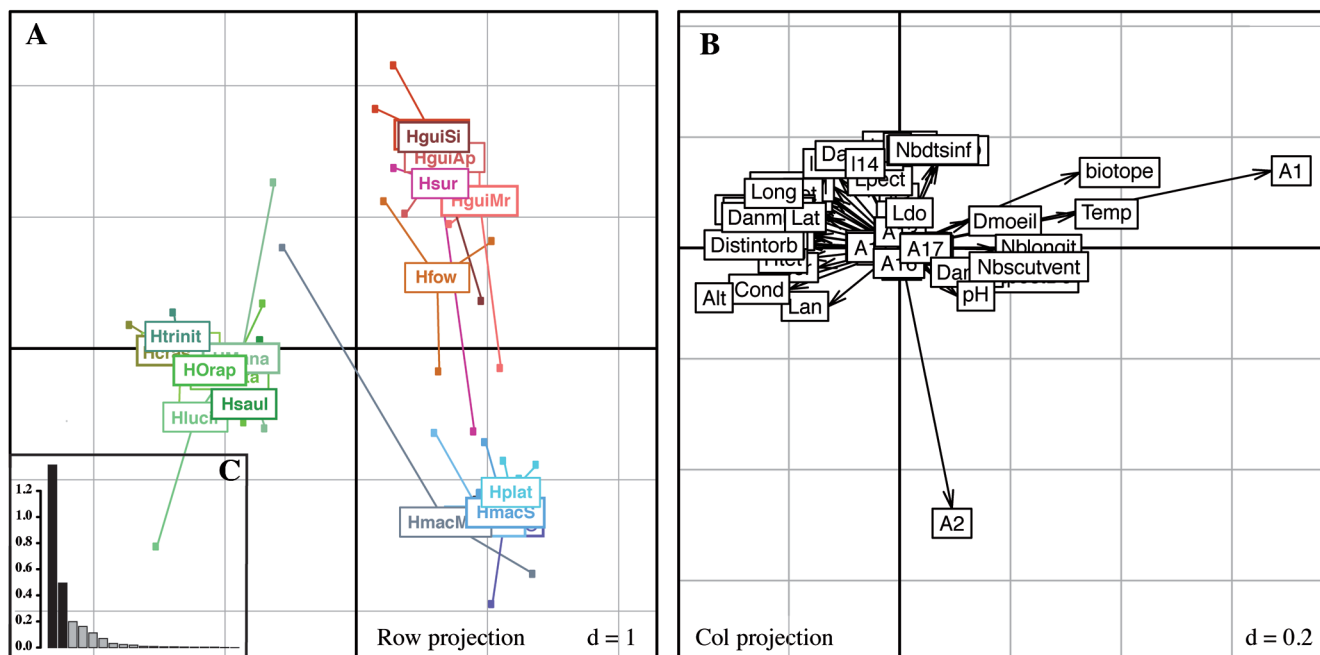


Figure 4. - Multiple co-inertia analysis. Projection of data coordinates of preliminary analyses (PCoA of genetic data and PCAs of morphological and ecology-distribution data) onto axes 1 and 2 of the multiple co-inertia analysis. **A**: Reference structure (labels) and superimposed normalized individuals' scores of preliminary analyses (dots) in the multiple co-inertia plane; populations and species labelled as in tables II and V, and the list of material. **B**: Coordinates of the variables in the first multiple co-inertia plane (labelled as in Tab. IV). **C**: Eigenvalues of the multiple co-inertia analysis.

## TAXONOMIC IMPLICATIONS

Based on these results, the systematics of Guianese Harttiini is revised. Due to the very strong genetic, morphological and ecological groupings, three valid genera are here recognized: *Cteniloricaria*, *Harttiella*, and *Harttia* (their diagnosis is presented later on in this chapter). Several populations within these three genera represent new taxa, and one synonymy is highlighted. For diagnoses of new species and redescrptions of formerly described species, all variables were submitted to an analysis of variance between species, and significant differences in mean were evaluated using the Tukey's Honest Significant Differences (HSD) post-hoc test using a 95% confidence interval. This single-step multiple comparison procedure allows to find which means are significantly different from one another. Prior to the analysis of variance, individuals' measurements were rank-transformed by species to reduce problems related to small samples.

### *Cteniloricaria* Isbrücker & Nijssen, 1979

*Cteniloricaria* Isbrücker & Nijssen, in Isbrücker, 1979: 91. Type species: *Loricaria platystoma* Günther,

1868. Type by original designation. Gender: Feminine.

*Cteniloricaria* is distinguished from all other Guianese Harttiini by 30 morphometric variables (Tab. V) among which, six possessed very strong loadings onto PCA axes (Fig. 1B). *Cteniloricaria* is characterized by a slender appearance with a greater postdorsal length representing on average  $61.53 \pm 1.14\%$  of SL vs  $56.91 \pm 1.36$  in *Harttia* (Tukey HSD, p-value < 0.0001) and  $51.18 \pm 2.96$  in *Harttiella* (HSD, p-value < 0.0001), a longer caudal peduncle [mean =  $51.69 \pm 1.16\%$  of SL vs  $47.88 \pm 1.39$  (HSD, p-value < 0.0001) and  $40.73 \pm 3.41$  (HSD, p-value < 0.0001) in *Harttia* and *Harttiella*, respectively], a greater anus to anal-fin origin length [mean =  $8.89 \pm 0.52\%$  of SL vs  $8.67 \pm 0.57$  (HSD, p-value = 0.004) and  $8.49 \pm 1.27$  (HSD, p-value < 0.0001) in *Harttia* and *Harttiella*, respectively], larger eye with a greater maximum orbital diameter [mean =  $23.40 \pm 2.11\%$  of HL vs  $22.80 \pm 1.50$  (HSD, p-value = 0.0016) and  $17.38 \pm 1.68$  (HSD, p-value < 0.0001) in *Harttia* and *Harttiella*, respectively], more numerous plates in the lateral series [mean =  $30 \pm 1$  vs  $29 \pm 1$  (HSD, p-value < 0.0001) and  $25 \pm 1$  (HSD, p-value < 0.0001) in *Harttia* and *Harttiella*, respectively], and a greater number of lat-

Table III. - Main characteristics of the multi-table analysis computed on the restricted data set (n = 19). Genetic: genetic data table; Morphology: morphometric data table; Ecology: ecology-distribution data table. Levelplot: graphical representation of the structure of each data set converted into distances matrix: K2P distances for the genetic data, and Euclidian distances for the morphometric and ecology-distribution data. CADM: test of congruence among distances matrices. Mantel.mean: correlation of each matrix with respect to the two other matrices. p-value: significance of the test for  $\alpha = 0.05$  using Holm's correction. Mantel correlations: pairwise Mantel correlations of the rank-transformed distances between matrices. MCOA: multiple co-inertia analysis. Inertia: maximum inertia projected onto the two first axes of the simple analyses (eigenvalues of the PCoA for the genetic data, and eigenvalues of PCAs for the morphometric and ecology-distribution data tables). Co-inertia: inertia of the three tables projected onto the two first multiple co-inertia axes. Cos<sup>2</sup>: correlation between the scores of each table and the synthetic variable of same rank (axes 1 and 2). Cov<sup>2</sup>: squared covariance between the scores of each table and the synthetic variable of same rank (maximized by the analysis); note that Cov<sup>2</sup> provides the contribution of each table to the compromise established by the multiple co-inertia analysis.


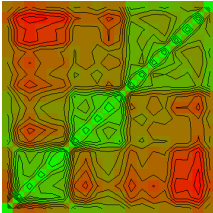
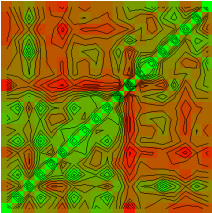
	Genetic	Morphology	Ecology
Levelplot			
CADM			
Mantel.mean	0.553	0.494	0.451
p-value	0.0003	0.0003	0.0003
Mantel correlations			
Genetic	1.000	0.596	0.509
Morphology	0.596	1.000	0.393
Ecology	0.509	0.393	1.000
MCOA			
Inertia			
Axis 1	0.486	0.608	0.458
Axis 2	0.251	0.215	0.175
Co-Inertia			
Axis 1	0.481	0.586	0.456
Axis 2	0.252	0.232	0.133
Cos <sup>2</sup>			
Axis 1	0.957	0.922	0.868
Axis 2	0.953	0.908	0.324
Cov <sup>2</sup>			
Axis 1	0.461	0.541	0.396
Axis 2	0.241	0.211	0.043

Table IV. - Tests against phylogenetic dependence of the variables constituting the different data sets. Variables: A1 to A5: five first eigenvalues of the PCoA of the K2P distances matrix; Ltet to Nbscutvent: morphometric variables labelled as in table 1; biotope to Long: ecology-distribution variables labelled as in figure 3. Axis 1: scores of the different variables onto the first multiple co-inertia axis; Axis 2: scores of the different variables onto the second multiple co-inertia axis; C-mean: Abouheif's measures of local autocorrelation corresponding to the degree to which related species are close from each other in a given trait; p-value: uncorrected significance of the Abouheif's test for  $\alpha = 0.05$ ; C p-value: corrected p-value using the control for false discovery rate for multiple testing under dependency.

Variable	Axis 1	Axis 2	C-mean	p-value ( $X \geq X_{obs.}$ )	C p-value ( $X \geq X_{obs.}$ )
A1	0.6719	0.1392	0.8457	0.0001	0.0011
A2	0.0944	-0.4704	0.7086	0.0001	0.0011
A3	-0.0010	0.0635	0.5478	0.0021	0.0115
A4	-0.0061	0.0314	0.4317	0.0005	0.0032
A5	0.0153	0.0018	0.4128	0.0060	0.0312
Ltet	-0.1406	0.0875	0.6830	0.0001	0.0011
Labd	-0.1216	0.0914	0.4795	0.0009	0.0052
LpreDo	-0.1691	0.0421	0.8059	0.0001	0.0011
LpostDo	0.1613	-0.0538	0.7392	0.0001	0.0011
LpostAn	0.1594	-0.0345	0.7275	0.0001	0.0011
Lmus	-0.1443	0.0819	0.7518	0.0001	0.0011
LnarBM	-0.1187	0.1103	0.6680	0.0001	0.0011
Lthor	-0.1549	0.0219	0.6527	0.0002	0.0018
Lpect	-0.0355	0.0950	0.2661	0.0383	0.1842
Lpelv	-0.1540	0.0222	0.6340	0.0002	0.0018
Ldo	0.0177	0.0370	0.0265	0.4021	1.0000
Lan	-0.1288	-0.1052	0.6790	0.0001	0.0011
ltet	-0.1392	0.0988	0.7495	0.0001	0.0011
lcorDo	-0.1088	0.1260	0.6606	0.0005	0.0032
lcorAn	0.0004	0.1574	0.5890	0.0002	0.0018
Hcor	-0.1473	-0.0354	0.4916	0.0010	0.0057
Htet	-0.1668	-0.0186	0.7478	0.0002	0.0018
HminPC	-0.1721	0.0082	0.8049	0.0001	0.0011
Hintnar	-0.1666	0.0244	0.7646	0.0001	0.0011
Dmoeil	0.1256	0.0487	0.5301	0.0005	0.0032
Distintorb	-0.1733	0.0055	0.8190	0.0001	0.0011
OpercBM	-0.1536	0.0690	0.7490	0.0001	0.0011
Danpelv	-0.0727	0.1403	0.5536	0.0006	0.0037
Danpect	-0.1565	0.0643	0.7682	0.0001	0.0011
Danan	0.0565	-0.0438	0.3310	0.0135	0.0666
Danmus	-0.1625	0.0552	0.7657	0.0001	0.0011
l8	-0.0042	0.1550	0.5470	0.0003	0.0024
l14	-0.0623	0.1259	0.5276	0.0008	0.0048
Nbdtssup	0.0688	0.1493	0.6088	0.0005	0.0032
Nbdtsinf	0.0613	0.1510	0.5865	0.0005	0.0032
Nblongit	0.1736	-0.0024	0.8200	0.0001	0.0011
Nbscutvent	0.1263	-0.0340	0.5362	0.0003	0.0024
biotope	0.3254	0.1362	0.6626	0.0003	0.0024
Temp	0.3174	0.0612	0.5407	0.0005	0.0032
pH	0.1044	-0.0868	-0.2344	0.9420	1.0000
Cond	-0.1991	-0.0745	0.2276	0.0796	0.3735
Alt	-0.3015	-0.0899	0.4825	0.0026	0.0139
Lat	-0.1332	0.0550	-0.0730	0.6673	1.0000
Long	-0.1745	0.0984	0.3917	0.0079	0.0400

eral abdominal plates [in mean  $8 \pm 2$  vs  $7 \pm 2$  (HSD, p-value = 0.0111) and  $6 \pm 1$  (HSD, p-value < 0.0001) in *Harttia* and *Harttiella*, respectively]. The following combination of characters also differentiates the genus: abdomen completely covered with medium sized rhombic plates, these plates becoming more numerous and decreasing in size toward the head; abdominal cover reaching gill opening, not organized in rows, and complete around 70 mm SL; presence of a black crescent in the caudal fin.

Within the *Cteniloricaria* group strong genetic divergences and morphological structures were found with significant differences in PCA scores for the first axis ( $\chi^2_{K-W} = 13.7128$ , p-value = 0.0175), but not for the second ( $\chi^2_{K-W} = 8.4508$ , p-value = 0.1331). No significant differences in shape ( $W = 1118$ , p-value = 0.1383), nor in genetics ( $K2P = 0.003$ ) were recorded between *C. platystoma* from Essequibo drainage [described from Suriname (Günther, 1868), but subsequently restricted to Guyana (Boeseman, 1971)] and *C. maculata* from Corantijn River (type locality, Sipaliwini River). As a consequence, *C. maculata* falls here into the synonymy of *C. platystoma*. This latter therefore includes all populations from the Essequibo in Guyana to the Sinnamary River in French Guiana, including Mana River (new record). All barcoded populations previously recorded as *C. maculata* fell within the usual range of populational variation of COI barcodes ( $\leq 0.03$ ). Populations from French Guiana nevertheless displayed stronger differences in genetics (0.017 to 0.026) and shape ( $W = 2930$ , p-value = 0.0161) with respect to Western populations. A shift between morphology and genetics was also observed with populations from Maroni, Mana, and Suriname Rivers exhibiting similar appearance ( $\chi^2_{K-W} = 0.1398$ , p-value = 0.9325), whereas genetically the latter was more closely related to populations from Corantijn and Essequibo Rivers (in mean 0.013 vs 0.025 K2P divergence). A population from Paru de Oeste River displayed strong genetic differences of specific level (K2P distances > 0.05), but displayed few morphometric differences compared to *C. platystoma*. Only 12 morphometric variables out of 32 distinguished significantly both species (Tab. V). The colour pattern also distinguished the population from Paru de Oeste River from the previous species.

### *Cteniloricaria platystoma* (Günther, 1868)

(Supplementary material S1)

*Loricaria platystoma* Günther, 1868: 478. Type locality: Surinam (?). Lectotype: BMNH 1866.8.14.124, designated by Isbrücker (1979: 113).

*Oxyloricaria platystoma* (Günther, 1868): Regan, 1904: 298.

*Parasturisoma platystoma* (Günther, 1868): Boeseman, 1971: 37.

*Cteniloricaria platystoma* (Günther, 1868): Isbrücker, 1979: 91; Isbrücker, 1980: 89; Burgess, 1989: 440; Isbrücker, 2001: 26, 29; Isbrücker, 2002: 15; Ferraris in Reis et al., 2003: 331; Ferraris,

2007: 233; Vari et al., 2009: 39.

*Harttia platystoma* (Günther, 1868): Eigenmann, 1912: 251; Rapp Py-Daniel and Oliveira, 2001: 80, Provenzano et al., 2005: 521; Covain et al., 2006: 17.

*Parasturisoma maculata* Boeseman, 1971: 33, pl. 5. Type locality: Sipaliwini, near airstrip, upper Corantijn River basin, Surinam. Holotype: RMNH 26381.

*Harttia maculata* (Boeseman, 1971): Rapp Py-Daniel and Oliveira, 2001: 80; Provenzano et al., 2005: 521; Covain et al., 2006: 9.

*Cteniloricaria maculata* (Boeseman, 1971): Isbrücker, 1979: 91; Burgess, 1989: 440; Le Bail et al., 2000: 268; Isbrücker, 2001: 26, 30; Isbrücker, 2002: 15; Ferraris in Reis et al., 2003: 331; Ferraris, 2007: 233.

Morphometric and meristic data are provided in table I, and GenBank accession numbers for barcodes in table II. Twelve morphometric variables distinguish *C. platystoma* from its congener (Tab. V). *Cteniloricaria platystoma* is distinguished from *C. napova* n. sp. by a greater postdorsal length (mean =  $61.60 \pm 1.14\%$  of SL vs  $60.73 \pm 0.74$ ; HSD, p-value = 0.006), longer caudal peduncle (mean =  $51.74 \pm 1.14\%$  of SL vs  $51.03 \pm 0.90$ ; HSD, p-value = 0.0191), and pelvic-fin spines (mean =  $18.10 \pm 1.01\%$  of SL vs  $17.53 \pm 0.42$ ; HSD, p-value = 0.0342), a wider body at eighth postdorsal plate (mean =  $9.34 \pm 0.97\%$  of SL vs  $8.85 \pm 0.58$ ; HSD, p-value = 0.0348), a greater nostril to tip of snout length (mean =  $39.16 \pm 2.70\%$  of HL vs  $36.86 \pm 1.93$ ; HSD, p-value = 0.009), and interorbital width (mean =  $22.50 \pm 1.11\%$  of HL vs  $21.51 \pm 1.29$ ; HSD, p-value = 0.0025). K2P distances to congeneric species ranged from 0.056 to 0.070 according to the population. Its colouration makes it difficult to observe in its natural habitat (Supplementary material S2). The background colour of the dorsal surface is brown with darker indistinct marbling forming black transverse bands toward the tail. Limits of plates are well defined and appear darker, particularly in the anterior region. Areas with golden to bronze shimmers are present below the eyes, eye copper-coloured. A black crescent is present in the caudal fin, sometimes extending toward the lower lobe making it almost black. A black colouration may be also present in the anterior and uppermost part of the dorsal fin. All fins but anal possess dark punctuation on rays forming stripes. The lower surface is yellowish tan. The teeth are not numerous for a Harttiini (around 40 on each jaw), pedunculated, and arranged in a single, comblike row. Sexual dimorphism has never been reported despite a large sampling effort. It could be therefore different from what is commonly reported for other Harttiini. Indeed, certain specimens exhibit much longer pectoral and dorsal fins, the pectoral spines sometimes bearing short but more developed odontodes on their external surface, compared to others of the same size collected at the same place. Such specimens may represent males, which typically exhibit this type of



Table V. – Tukey's Honest Significant Differences post-hoc tests between genera (black dots) and within genera-between species (grey dots) for all morphometric variables. Presence of dots refers to significant differences in mean for the genus under consideration (or the species of a given genus), against all other genera (or species belonging to the same genus). Variables labelled as in table I. Labels refer to the labels used in the analyses for the different populations of a species and the different species.

--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

feature in other species. If it is confirmed, the lectotype of *C. platystoma* represents thus a male specimen, whereas the holotype of *C. maculata* corresponds to a female. This is a widespread species distributed in almost all Atlantic coastal drainages from Essequibo in Guyana to Sinnamary in French Guiana (Fig. 5). It is an inhabitant of the main channel of rivers where it colonizes rocky and sandy areas, in fast flowing waters. The species is locally abundant, particularly in its western distribution where it forms the only representative of the Harttiini. When it is sympatric with other Harttiini such as *Harttia surinamensis* or *H. guianensis*, its occurrence becomes scarcer, probably due to competitive exclusion, and it is more frequently observed in the marginal areas of its preferred biotopes, or even in forest creeks.

### *Cteniloricaria napova* Covain & Fisch-Muller, new species (Figs 5, 6; Tabs I, II)

#### Holotype

MZUSP 108146 (ex MHNG 2704.030, specimen SU07-667), 113.20 mm SL, Sipaliwini Savannah in Trio Amerindian territory at the Suriname-Brazil border, Four Brothers Mountains in a tributary of the Paru de Oeste River, gift of the Trio tribe in Sipaliwini, 20-21 Oct. 2007.

#### Paratypes

MHNG 2704.030 (6); MZUSP 108147 (2, ex MHNG 2704.030); MNHN 2011-0017 (2, ex MHNG 2704.030); National Zoological Collection of Suriname (NZCS) NZCS F7071 (1, ex MHNG 2704.030), same data as holotype.

#### Diagnosis

*C. napova* is distinguished from *C. platystoma*, its only congener, by its distinctly spotted colour pattern vs indistinctly marbled, and its specific barcode sequence (JF292256). Additionally, it is distinguished by a greater predorsal length (mean =  $30.91 \pm 0.38\%$  of SL vs  $29.91 \pm 0.90$  in *C. platystoma*; HSD, p-value < 0.0001), anus to pectoral-fin origin length (mean =  $23.92 \pm 0.89\%$  of SL vs  $23.31 \pm 0.93$ ; HSD, p-value = 0.0429), body width at dorsal-fin origin (mean =  $15.17 \pm 0.61\%$  of SL vs  $14.62 \pm 0.91$ ; HSD, p-value = 0.0228), body depth at dorsal-fin origin (mean =  $10.04 \pm 0.69\%$  of SL vs  $9.16 \pm 1.00$ ; HSD, p-value = 0.0012), head depth (mean =  $42.21 \pm 2.37\%$  of HL vs  $40.83 \pm 2.85$ ; HSD, p-value = 0.029), and more

numerous premaxillary teeth (mean =  $47 \pm 6$  vs  $40 \pm 12$ ; HSD,  $p$ -value = 0.0099).

### Description

Morphometric and meristic data in table I, and GenBank accession number in table II.

General aspect of fish slender and depressed, especially posterior to dorsal fin. Head triangular in dorsal view, with sides straight and snout slightly rounded. Eye large, orbit round, smooth, without notch. Odontodes very short, making fish rather smooth. Snout tip naked.

Mouth elliptic with large upper and lower lips. One buccal papilla. Surface of lips papillose, papillae numerous. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $> 40$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle large and triangular densely covered by odontodes. Abdomen completely covered by medium to small rhombic plates between lateral abdominal plates. Plates reaching gill opening, decreasing in size and becoming more numerous toward pelvic girdle. Abdominal plates not or poorly organized in rows. Throat not covered. Two large preanal plates. Seven to 11 (modally 7) lateral abdominal plates, plates keeled but not sharp. Thirty plates in median lateral series, plates keeled, coalescing in last nine to ten plates. Caudal peduncle becoming slightly more compressed in the last 10 plates.

Posterior margin of dorsal fin straight, generally with first and second branched ray longest. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than branched rays, reaching beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, reaching to or slightly beyond anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin deeply forked with i,12,i rays.

### Colouration

In alcohol, background colour of dorsal surface of head and body tan with numerous distinct small equally spaced dark spots. Anterior part of body, between pectoral fins, darker. Dark shading extending on the sides, but not onto the back, anterior of the pelvic fins. Ventral surface uniformly pale yellowish, appearing greyish in the transparent portion of the abdominal region due to dark pigmentation of internal organs. Dorsal-fin rays yellowish tan with numerous dark brown spots arranged in bands, with a black blotch on the tip. Caudal fin with a dark crescent in its middle part and dark stripes on its lower and upper lobes. Pectoral, pelvic, and anal fins lighter, with indistinct dark markings.

### Sexual dimorphism

Unknown. Maybe reminiscent of *C. platystoma* (see above).

### Distribution and habitat

Known from upper Paru de Oeste River (Fig. 5).

### Etymology

The species group name *napova* is from the Amerindian Trio-Wayana meaning thank you. It honours the Trio people from Sipaliwini who offered us these fish. Name used in apposition.

### Harttiella Boeseman, 1971

*Harttiella* Boeseman, 1971: 25. Type species: *Harttia crassicauda* Boeseman, 1953. Type by original designation. Gender: Feminine.

*Harttiella* is distinguished from all other Guianese Harttiini by 30 morphometric variables (Tab. V) among which, 18 possessed very strong loadings onto PCA axes (Fig. 1B). *Harttiella* is differentiated from other Guianese Harttiini by: a longer head respectively to its size [mean =  $25.00 \pm 1.51\%$  of SL vs  $23.70 \pm 1.35$  (HSD,  $p$ -value  $< 0.0001$ ) and  $21.13 \pm 1.18$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively]; greater predorsal length [mean =  $37.56 \pm 1.66\%$  of SL vs  $32.64 \pm 1.10$  (HSD,  $p$ -value  $< 0.0001$ ) and  $29.99 \pm 0.91$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], abdominal length [mean =  $18.89 \pm 1.30\%$  of SL vs  $17.83 \pm 1.09$  (HSD,  $p$ -value  $< 0.0001$ ) and  $16.61 \pm 1.02$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], thoracic length [mean =  $20.78 \pm 2.27\%$  of SL vs  $17.61 \pm 0.92$  (HSD,  $p$ -value  $< 0.0001$ ) and  $15.99 \pm 0.94$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], pelvic-spine length [mean =  $22.11 \pm 2.60\%$  of SL vs  $18.75 \pm 1.26$  (HSD,  $p$ -value  $< 0.0001$ ) and  $18.06 \pm 0.99$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], anal-spine length [mean =  $16.58 \pm 1.76\%$  of SL vs  $12.80 \pm 1.02$  (HSD,  $p$ -value  $< 0.0001$ ) and  $14.40 \pm 1.19$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], anus to pelvic-fin origin length [mean =  $11.36 \pm 1.60\%$  of SL vs  $10.76 \pm 0.89$  (HSD,  $p$ -value = 0.0003) and  $8.76 \pm 0.59$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], anus to pectoral-fin origin length [mean =  $31.09 \pm 3.13\%$  of SL vs  $26.26 \pm 1.12$  (HSD,  $p$ -value  $< 0.0001$ ) and  $23.35 \pm 0.94$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], and anus to tip of snout length [mean =  $47.03 \pm 2.92\%$  of SL vs  $40.55 \pm 1.35$  (HSD,  $p$ -value  $< 0.0001$ ) and  $36.83 \pm 0.90$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively]; a wider body at dorsal-fin origin [mean =  $20.25 \pm 2.89\%$  of SL vs  $18.78 \pm 1.39$  (HSD,  $p$ -value  $< 0.0001$ ) and  $14.66 \pm 0.90$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively]; a deeper body at dorsal-fin origin [mean =  $12.13 \pm 2.38\%$  of SL vs  $8.75 \pm 0.83$  (HSD,  $p$ -value  $< 0.0001$ ) and  $9.22 \pm 1.00$  (HSD,  $p$ -value  $< 0.0001$ ) in *Harttia* and *Cteniloricaria*, respectively], and deeper cau-



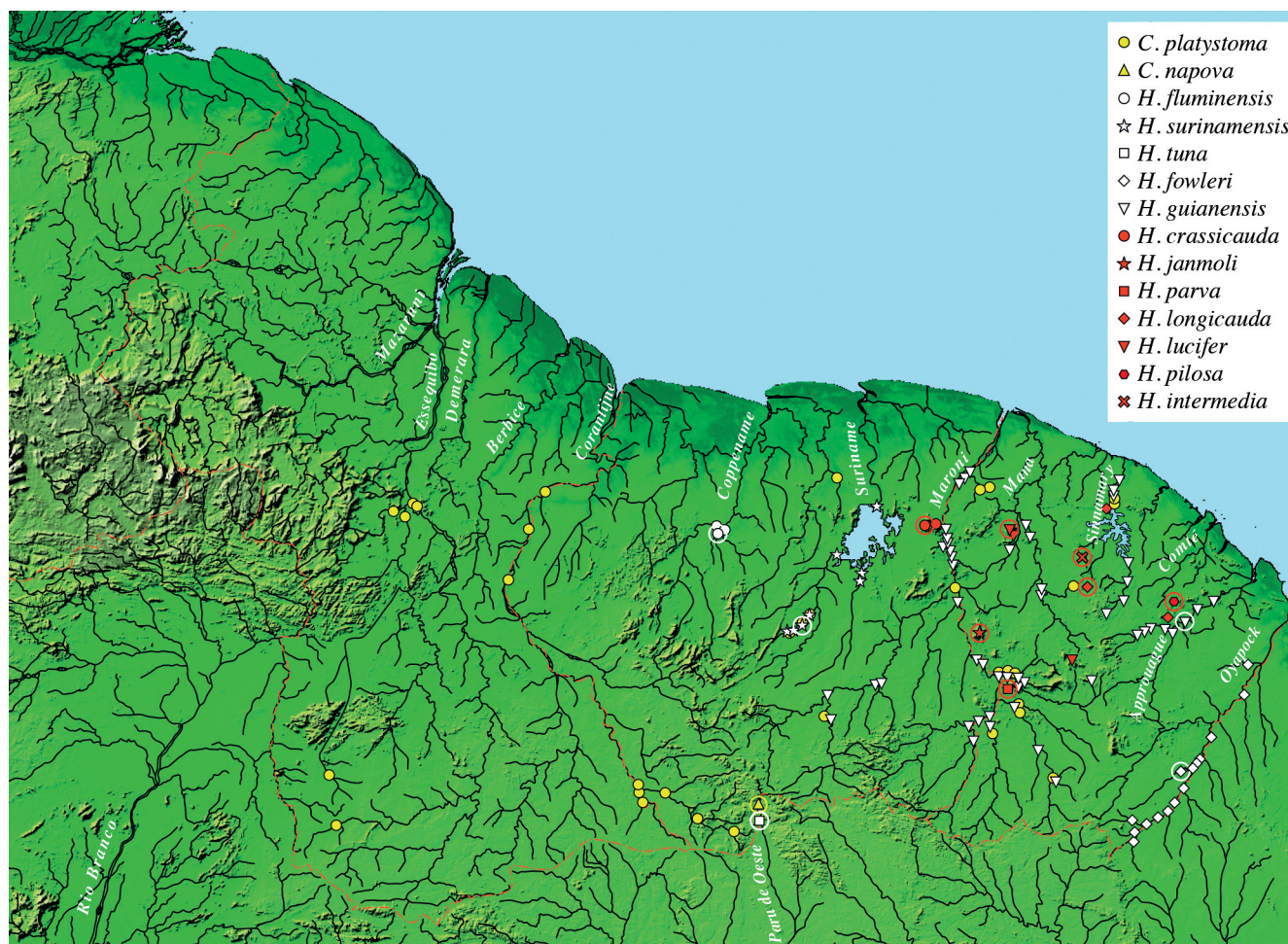


Figure 5. - Geographic distribution of Guianese Harttiini; circled symbols refer to type localities. The map takes into account present results and updates previous records and known distributions accordingly.

dal peduncle [mean =  $3.75 \pm 0.99\%$  of SL vs  $1.41 \pm 0.14$  (HSD, p-value < 0.0001) and  $1.13 \pm 0.09$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively]; a longer snout [mean =  $59.39 \pm 3.34\%$  of HL vs  $56.32 \pm 2.95$  (HSD, p-value < 0.0001) and  $53.52 \pm 3.07$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively]; a wider head [mean =  $99.62 \pm 6.94\%$  of HL vs  $93.77 \pm 6.74$  (HSD, p-value < 0.0001) and  $82.76 \pm 4.93$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively]; a greater distance from the distal end of operculum to tip of snout [mean =  $84.71 \pm 3.67\%$  of HL vs  $79.87 \pm 2.53$  (HSD, p-value < 0.0001) and  $77.77 \pm 2.25$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively], and interorbital width [mean =  $35.29 \pm 2.12\%$  of HL vs  $22.53 \pm 1.34$  (HSD, p-value < 0.0001) and  $22.43 \pm 1.15$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively]; a deeper head [mean =  $46.09 \pm 4.12\%$  of HL vs  $36.94 \pm 2.72$  (HSD, p-value < 0.0001) and  $40.93 \pm 2.83$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively], and greater head depth at internostril [mean =  $34.16 \pm 2.83\%$  of HL

vs  $28.90 \pm 2.62$  (HSD, p-value < 0.0001) and  $29.62 \pm 2.55$  (HSD, p-value < 0.0001) in *Harttia* and *Cteniloricaria*, respectively]. The following combination of characters also differentiates the genus: abdomen naked with exception of lateral abdominal plates and, rarely, preanal plates; small size (largest known specimen reached 52.46mm SL); body densely covered by odontodes; subpreopercle not exposed; lateral plates not keeled.

Within the *Harttiella* group, significant morphological structures were recovered by axes one and two of the PCA ( $\chi^2_{K-W} = 181.7766$ , p-value < 0.0001;  $\chi^2_{K-W} = 137.4764$ , p-value < 0.0001), as well as deep genetic divergences ( $0 \leq K2P \leq 0.119$ ). Two main morphological tendencies were highlighted on both axes by the morphometric study, with on one hand stockier forms constituting a first group named the *crassicauda* group, and on the other hand slender representatives forming a second group named the *longicauda* group ( $W = 37$ , p-value < 0.0001;  $W = 1321$ , p-value < 0.0001). The *crassicauda* group included the type species *H. crassicauda* and populations from the Kotika, Atachi Bakka and



Figure 6. - *Cteniloricaria napova*, holotype, MZUSP 108146, 113.20 mm SL, Sipaliwini Savannah in Trio Amerindian territory at the Suriname-Brazil border, Four Brothers Mountains in a tributary of the Paru de Oeste River.

Trinité Mountains. The four populations constituting the *crassicauda* group were morphologically significantly distinct ( $\chi^2_{K-W} = 56.3771$ , p-value < 0.0001;  $\chi^2_{K-W} = 15.6406$ , p-value = 0.0013 for axis 1 and 2 respectively), and possessed deep genetic divergences ( $0.031 \leq K2P \leq 0.051$ ) of interspecific level for the three barcoded populations. These four populations therefore constitute distinct species. Surprisingly, the population from Trinité Mountains that belonged to the *crassicauda* group, displayed almost no genetic divergence with populations from Crique Aya, and Cascades (from 0.003 to 0.005 K2P divergence respectively) both belonging to the *longicauda* group, whereas it showed strong morphological differences to them ( $W = 7$ , p-value = 0.0004;  $W = 31$ , p-value = 0.0027 for axes 1 and 2). The genetic divergence between Aya and Cascades was 0.0017 implying populational variations. Little morphometric variation was nevertheless recorded for the first axis but not for the second ( $\chi^2_{K-W} = 6.5204$ , p-value = 0.0384;  $\chi^2_{K-W} = 0.5922$ , p-value = 0.7437), and included three populations: Crique Aya (Mana drainage), Crique Cascades (Approuague drainage), and Crique Coeur Maroni (Sinamary drainage). Within the *longicauda* group, the popu-

lations from Lucifer massif (Mana drainage) and Crique Limonade (Maroni drainage) possessed very similar mitochondrial signature ( $0 \leq K2P \leq 0.002$ ) as well as little morphological differentiation on the first axis ( $W = 14$ , p-value = 0.0077;  $W = 38$ , p-value = 0.3917). These two populations correspond thus to a single species that possesses the strongest genetic divergence with congeneric representatives ( $0.112 \leq K2P \leq 0.119$ ). The population from Crique Grillon (Orapu drainage) appeared genetically closer to representatives of the *crassicauda* group (mean K2P divergence to *crassicauda* group = 0.039 vs 0.090 with representatives of the *longicauda* group). All genetic variations corresponded to the between species level ( $> 0.03$ ). Significant morphological tendencies were also highlighted by the PCA between the population from Orapu and those from Aya, Cascades, and Coeur Maroni creeks ( $W = 222$ , p-value = 0.0408;  $W = 122$ , p-value = 0.0005 for the two first axes). Nevertheless, this population appeared morphologically close to the forms from Lucifer massif and Crique Limonade ( $W = 131$ , p-value = 0.8848 for axis 1,  $W = 188$ , p-value = 0.023 for axis 2).



***Harttiella crassicauda* (Boeseman, 1953)**

(Supplementary material S3)

*Harttia crassicauda* Boeseman, 1953: 10, Figs 1b, 2. Type locality: Nassau Mountains, in creek, Suriname. Holotype: RMNH 19418 (largest of 15 specimens), not separated from paratypes.

*Harttiella crassicauda* (Boeseman, 1953): Boeseman, 1971: 11; Isbrücker, 1980: 89; Burgess, 1989: 439; Le Bail *et al.*, 2000: 276; Isbrücker, 2001: 27; Isbrücker, 2002: 16; Ferraris *in* Reis *et al.*, 2003: 336; Ferraris, 2007: 242; Vari *et al.*, 2009: 39.

Morphometric and meristic data are provided in table I, and GenBank accession numbers for barcodes in table II. Four morphometric variables significantly characterize *H. crassicauda* (Tab. V). *Harttiella crassicauda* is distinguished from all other congeneric species by a smaller postdorsal length [mean =  $48.05 \pm 0.92\%$  of SL vs  $48.85 \pm 1.33 < \text{mean} < 53.89 \pm 1.41\%$  of SL in all other congeners; (HSD, p-values  $< 0.0261$ )], a shorter caudal peduncle [mean =  $36.14 \pm 1.66\%$  of SL vs  $38.32 \pm 1.54 < \text{mean} < 43.94 \pm 0.90\%$  of SL in all other congeners; (HSD, p-values  $< 0.0001$ )], and a deeper caudal peduncle [mean =  $4.86 \pm 0.43\%$  of SL vs  $2.53 \pm 0.18 < \text{mean} < 4.58 \pm 0.35\%$  of SL in all other congeners; (HSD, p-values  $< 0.0015$ )]. It is also distinguished from all other congeneric species except *H. janmoli* n. sp. by a greater (smaller compared to *H. janmoli*) anus to pectoral-fin origin length [mean =  $31.85 \pm 2.26\%$  of SL vs  $28.38 \pm 2.75 < \text{mean} < 29.23 \pm 1.81\%$  of SL in other congeners; (HSD, p-values  $< 0.0067$ ), and mean =  $34.24 \pm 1.67\%$  of SL in *H. janmoli* (HSD, p-value = 0.0179)]. K2P distances to congeneric species ranged between 0.031 and 0.119 according to the species. No differences (K2P = 0) were recorded between the two barcoded populations of Paramaka Creek. The general appearance of the species is broad, with a triangular head, and a short and thick caudal peduncle. The background colouration in dorsal view is brown, generally with five narrow dark brown transverse bands posterior to dorsal-fin insertion. Some indistinct dark spotting may also be present between the postdorsal bands. The anterior part of the body is indistinctly marbled, conferring the species camouflage with the substrate (Supplementary material S4-A). Fin rays also have darker markings, more or less forming stripes. Ventral surface is lighter. The sexual dimorphism consists in the hypertrophy of odontodes on the entire body, and particularly on the S-shaped pectoral-fin spines and around the snout in males.

*Harttiella crassicauda* is only known from Nassau Mountains in Suriname (Fig. 5), where it occurs in the upper reaches of Paramaka Creek, a tributary of Marowijne River, at an altitude up to 250 m above mean sea level. It has not been collected in streams to the north (Anjoemara Creek) or to the south (Gran Creek) of Paramaka Creek. The reaches with *H. crassicauda* were shallow (mainly  $< 50$  cm water depth), but with year-round running water (e.g., *H. crassicauda* was not collected in the extreme headwaters of Paramaka Creek which fall dry in the long dry season September–November).

The bottom substrate consisted of bedrock, boulders, pebbles, gravel and sometimes large-grain sand. The water was clear (Secchi transparency  $> 200$  cm in deep pools at the edge of the plateau), slightly acidic (pH 5.1–6.9), with low conductivity ( $23\text{--}28 \mu\text{S/cm}$ ), variable current velocity ( $0\text{--}70$  cm/s), and relative low temperature ( $22.2\text{--}23.2^\circ\text{C}$ ) (Mol *et al.*, 2007). The upper reaches of Paramaka Creek had no aquatic vegetation except for some clumps of filamentous red algae (mainly *Batrachospermum* spp.) and stands of the emergent *Thurnia sphaerocephala* at the edge of the plateau. Other fish species of these high-altitude streams in Nassau Mountains included: *Rivulus* cf. *igneus*, *Synbranchus marmoratus*, *Callichthys callichthys*, *Lithoxus* spp., an unidentified trichomycterid catfish, and a *Guyanancistrus* species (see this volume).

The extremely limited distribution of *H. crassicauda* in a single creek on a single mountain, coupled with the small population sizes, make it highly vulnerable. Urgent measures should be taken to protect this species and its immediate environment, which is directly endangered by mining activities in Nassau Mountains.

***Harttiella pilosa* Covain & Fisch-Muller, new species**

(Figs 5, 7; Tabs I, II)

**Holotype**

MHNG 2724.004 (ex-MHNG 2682.055, specimen GF06-338), 39.91 mm SL, French Guiana, Tortue Mountains, Orapu River drainage in Crique Grillon at the ONF camp, Covain *et al.*, 8 Nov. 2006.

**Paratypes**

MNHN 2011-0018 (4, ex MHNG 2682.055); MHNG 2682.055 (4); NZCS F7072 (1, ex MHNG 2682.055); same data as holotype. MHNG 2724.002 (1), French Guiana, Tortue Mountains, Orapu River drainage in Crique Grillon at the ONF camp, Vigouroux *et al.*, 7 Nov. 2003.

**Diagnosis**

*Harttiella pilosa* is distinguished from all other *Harttiella* by its hispid appearance, vs smooth to velvety in congeneric species, and its specific barcode sequences (JF292271, JF292272, JF292273). No morphometric variable strictly distinguishes *H. pilosa* from all other congeners (Tab. V). It can be distinguished from species belonging to the *crassicauda* group by a shorter head [mean =  $23.74 \pm 1.35\%$  of SL vs  $25.54 \pm 1.41 < \text{mean} < 26.18 \pm 1.34\%$  of SL; (HSD, p-values  $< 0.0033$ )], and from other species of the *longicauda* group by a deeper body at dorsal-fin origin [mean =  $11.92 \pm 0.97\%$  of SL vs  $9.86 \pm 0.79 < \text{mean} < 10.66 \pm 0.87\%$  of SL; (HSD, p-values  $< 0.0069$ )].

### Description

Morphometric and meristic data in table I, and GenBank accession numbers in table II.

A member of the *longicauda* group. General aspect of fish small, slender and hairy, especially anterior to dorsal-fin origin. Caudal peduncle, long and slender. Anterior margin of head rounded in dorsal view. Eye small, orbit round, without notch. Odontodes short and thick, densely covering body making fish rather hispid or slightly spiny particularly in males. Snout tip naked.

Mouth elliptic with large and thick upper and lower lips. One buccal papilla. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 40$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle not visible in ventral view. Abdomen naked except for lateral abdominal plates, and sometimes preanal plates in larger specimens. Six to 8 (modally 6) lateral abdominal plates, plates keeled but not sharp. Twenty-six plates in median lateral series, plates not coalescing.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than soft rays, reaching slightly beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, reaching anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin truncated with i,12,i rays.

### Colouration

In alcohol, background colour of dorsal surface of head and body greyish brown with 4 to 5 dark saddles posterior to dorsal-fin origin. On side of body, saddles have form of indistinct blotches. Anterior part of body darker. Ventral surface lighter. Lower caudal peduncle dingy off-yellow with dark marks. Black blotch at base of anal and pelvic fins. Fin rays yellowish tan with dark brown spots. Fins membranes hyaline. Caudal fin with indistinct dark markings.

In life, background colour of dorsal surface reddish brown, with black postdorsal bands (Supplementary material S4-B).

### Sexual dimorphism

Males with longer, thicker and more widely spaced apart odontodes on the head surface, and on pectoral spines, and with a deeper snout, particularly at the level of internostril.

### Distribution and habitat

Only known from type locality. *Harttiella pilosa* was collected in Crique Grillon, a tributary of Orapu River in Tortue Mountains (Fig. 5), at an altitude of approximately 200 m above mean sea level. The portion of the river in which *H. pilosa* was found was immediately upstream of a 30 m high waterfall (*H. pilosa* was not collected downstream of

the waterfall). That portion of the river was approximately 10 m wide with shallow (5–40 cm) water and a bottom substrate consisting of gravel, pebbles, boulders, bed rock and sand mainly constituted of iron hydroxide (Edwin Gnos, MHNG, pers. comm.). Leaf litter and large woody debris were also abundant. The water was clear (Secchi transparency  $> 40$  cm), slightly acidic (pH 6.5), with low conductivity ( $52 \mu\text{S}/\text{cm}$ ), variable current (0–70 cm/s), and relatively low temperature ( $24^\circ\text{C}$ ). The reach had no aquatic macrophytes, but clumps of filamentous red algae were observed on rocky bottom substrate. The fish community included: *Bryconops affinis*, *Hemigrammus unilineatus*, *Melanocharacidium blennioides*, *Helogenes marmoratus*, *Pseudopimelodus raninus*, *Ancistrus* cf. *leucostictus*, *Lithoxus planquettei*, *Guyanancistrus* aff. *brevispinis*, *Krobia guianensis*, and *Crenicichla* sp.

### Etymology

The species group name *pilosa* is from Latin *pilosus* meaning hairy, and makes reference to the unusual aspect of male head.

### *Harttiella parva* Covain & Fisch-Muller, new species

(Figs 5, 8; Tabs I, II)

#### Holotype

MNHN 2011-0019 (ex MHNG 2723.093, specimen MUS-607), 29.54 mm SL, French Guiana, Atachi Bakka Mountains, Maroni River drainage, Gaucher, Jun. 2009.

#### Paratypes

MNHN 2011-0020 (2, ex MHNG 2723.093); MHNG 2723.093 (3), same data as holotype.

#### Diagnosis

*Harttiella parva* is distinguished from all other *Harttiella* by its small size with sexual dimorphism expressed around 25 mm SL (vs around 30 mm SL in congeneric species), by the distinct banded colour pattern of the caudal fin (vs blotched or indistinct banded pattern in congeneric species), and by its specific barcode sequences (JF292274, JF292275, JF292276). *Harttiella parva* does not show unique morphometric tendencies distinguishing it from all other congeneric species (Tab. V). It is distinguished from other congeners except *H. intermedia* n. sp. by a caudal peduncle: shorter compared to the species belonging to the *longicauda* group [mean =  $40.36 \pm 1.06\%$  of SL vs  $43.61 \pm 1.79 < \text{mean} < 44.26 \pm 1.48\%$  of SL; (HSD, p-values  $< 0.0002$ )], and longer compared to the other species of the *crassicauda* group [mean =  $40.36 \pm 1.06\%$  of SL vs  $36.14 \pm 1.66 < \text{mean} < 38.32 \pm 1.54\%$  of SL; (HSD, p-values  $< 0.0281$ )]. It is distinguished from *H. intermedia* by a smaller body depth at dor-



Figure 7. - *Harttiella pilosa*, holotype, MHNG 2724.004, 39.91 mm SL, French Guiana, Tortue Mountains, Orapu River drainage in Crique Grillon at the ONF camp.

sal-fin origin [mean =  $10.34 \pm 0.83\%$  of SL vs  $12.69 \pm 0.54$ ; (HSD, p-value = 0.0041)].

#### Description

Morphometric and meristic data in table I, and GenBank accession numbers in table II.

A member of the *crassicauda* group. General aspect of fish small and stocky, with a short, broad and thick caudal peduncle. Head rounded in dorsal view. Eye small, orbit round, without notch. Odontodes short, densely covering body, conferring fish a velvety aspect. Snout tip naked.

Mouth elliptic with large upper and lower lips. One buccal papilla. Surface of lips papillose, with numerous papillae.

Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 40$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle not visible in ventral view. Abdomen naked except for lateral abdominal plates. Five to 7 (modally 6) lateral abdominal plates, plates keeled but not sharp. Twenty-four to 25 (modally 25) plates in median lateral series, plates not coalescing.

Dorsal fin originates more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than soft rays, S shaped, reaching slightly beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine long-



er, reaching beyond anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin truncated with i,12,i rays.

#### Colouration

In alcohol, background colour of dorsal surface of head and body brownish tan with 4 thin postdorsal dark bands. Anterior part of body darker. Ventral surface lighter. Fin rays yellowish tan with dark brown spots forming stripes. Fin membranes hyaline. Uppermost part of dorsal fin sometime with a small black blotch. Caudal fin with distinct dark stripes (usually 4) becoming larger toward distal margin. Last stripe forming a large black band at tail extremity.

#### Sexual dimorphism

Males with long and thicker odontodes on the external surface of pectoral spines.

#### Distribution and habitat

Only known from type locality (Fig. 5), a small forest creek in Atachi Bakka Mountains.

#### Etymology

The species group name *parva* is from Latin *parvus* meaning small, and makes reference to the size of the species.

#### **Harttiella intermedia** Covain & Fisch-Muller, new species (Figs 5, 9; Tabs I, II)

#### Holotype

MNHN 2011-0021 (ex MHNG 2713.087 specimen MUS-650), 34.67 mm SL, French Guiana, Sinnamary River drainage, Tabular Mountain of Trinité massif, Crique Grand Leblond, 4°36'35"N-53°21'33"W, alt. 320 m, Tostain and Ravet, 6 Oct. 2009.

#### Paratypes

MNHN 2011-0022 (2, ex MHNG 2713.087); MHNG 2713.087 (2), same data as holotype.

#### Diagnosis

*Harttiella intermedia* is distinguished from all other *Harttiella* by its stocky body shape reminiscent of the *crassicauda* group, and by its mitochondrial barcode signature typical for the *longicauda* group (JF292281, JF292284, JF292285). No unique morphometric data characterize *H. intermedia* (Tab. V). It is distinguished from *H. parva* plus representatives of the *longicauda* group except *H. pilosa* by a deeper body at dorsal-fin origin [mean =  $12.69 \pm 0.54\%$  of SL vs  $9.86 \pm 0.79 < \text{mean} < 10.66 \pm 0.87\%$  of SL; (HSD, p-values < 0.0041)], and from *H. janmoli* n. sp. by a shallower body at dorsal-fin origin [mean =  $12.69 \pm 0.54\%$  of SL vs  $14.80 \pm 1.14\%$  of SL; (HSD, p-value = 0.015)]. It is distinguished from *H. pilosa* by a longer head

[mean =  $26.18 \pm 1.12\%$  of SL vs  $23.74 \pm 1.35\%$  of SL; (HSD, p-value = 0.0031)], and from *H. crassicauda* by a longer caudal peduncle [mean =  $42.35 \pm 1.44\%$  of SL vs  $36.14 \pm 1.66\%$  of SL; (HSD, p-value < 0.0001)].

#### Description

Morphometric and meristic data in table I, and GenBank accession numbers in table II.

A member of the *crassicauda* group. General aspect of fish small and stocky, with a short, broad and thick caudal peduncle. Head rounded to slightly triangular in dorsal view. Eye small, orbit round, without notch. Odontodes short, densely covering body, conferring fish with a velvety aspect. Snout tip naked.

Mouth elliptic with large upper and lower lips. One buccal papilla. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 50$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle not visible in ventral view. Abdomen naked except for lateral abdominal plates. Five to 8 (modally 6) lateral abdominal plates, plates keeled but not sharp. Twenty four to 25 (modally 25) plates in median lateral series, plates not coalescing.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than branched rays, straight, reaching beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, reaching beyond anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin truncated with i,12,i rays.

#### Colouration

In alcohol, background colour of dorsal surface of head and body brownish tan with 5 thick postdorsal dark bands. Anterior part of body darker. Ventral surface lighter. Fin rays yellowish tan with indistinct dark brown spots more or less forming stripes. Fins membranes hyaline. Caudal fin with usually four indistinct dark stripes. Tip of caudal fin whitish. Some specimens with a basicaudal spot.

#### Sexual dimorphism

Unknown. Probably similar to that observed in *H. crassicauda* (see above).

#### Distribution and habitat

Only known from type locality (Fig. 5), in headwaters of Crique Grand Leblond on the Tabular Mountain of the Trinité Massif. The species was collected with representatives of *Ituglanis nebulosus*, *Rivulus igneus*, *R. lungi*, and *R. aff. breviceps*.





Figure 8. - *Harttiella parva*, holotype, MNHN 2011-0019, 29.54 mm SL, French Guiana, Atachi Bakka Mountains, Maroni River drainage.

#### Etymology

The species group name *intermedia* is from the Latin *intermedius* meaning intermediary, making reference to the contradiction between morphometry and genetics.

#### ***Harttiella lucifer* Covain & Fisch-Muller, new species** (Figs 5, 10; Tabs I, II)

#### Holotype

MNHN 2011-0023 (ex MHNG 2721.088 specimen GF10-034), 42.68 mm SL, French Guiana, Mana River drainage, Lucifer Mountains, West of Crique Cascade, 4°47'44.7"N-53°55'49.4"W, alt. 450 m, Montoya-Burgos and Fischer, 10 Feb. 2010.

#### Paratypes

MNHN 2011-0024 (4, ex MHNG 2721.088); MHNG 2721.088 (4); NZCS F7073 (1, ex MHNG 2721.088), same data as holotype. MNHN 2011-0025 (3, ex MHNG 2721.091), MHNG 2721.091 (3), NZCS F7074 (1, ex MHNG 2721.091), French Guiana, Mana River drainage, headwater of a creek in Lucifer massif flowing toward Citron, 4°45'54"N-53°56'14.9"W, alt. 365 m., Montoya-Burgos and Fischer, 11 Feb. 2010. MNHN 2011-0026 (4, ex MHNG 2712.085 specimens), MHNG 2712.085 (4), French Guiana, Maroni River drainage, Galbao Mountains in a tributary of Crique Limonade, 3°35'56.6"N-53°15'12.6"W, alt. 202 m., Tostain, 18 Mar. 2008.

### Diagnosis

No unique character distinguishes *Harttiella lucifer* from all other congeneric species (Tab. V) except its barcode sequence, the most divergent of all *Harttiella* representatives (JF292286 to JF292296). Compared to congeneric species of the *crassicauda* group except *H. intermedia*, *H. lucifer* possesses a longer caudal peduncle [mean =  $44.26 \pm 1.48\%$  of SL vs  $36.14 \pm 1.66 < \text{mean} < 40.36 \pm 1.06\%$  of SL; (HSD, p-values < 0.0001)]. Compared to other representatives of the *longicauda* group, *H. lucifer* is characterized by a greater cleithral width [mean =  $101.65 \pm 3.28\%$  of HL vs  $94.50 \pm 4.00 < \text{mean} < 95.78 \pm 4.04\%$  of HL; (HSD, p-values < 0.002)]. It is distinguished from *H. intermedia* by a smaller predorsal length [mean =  $35.95 \pm 1.19\%$  of SL vs  $37.93 \pm 1.07\%$  of SL; (HSD, p-value = 0.0049)].

### Description

Morphometric and meristic data in table I, and GenBank accession numbers in table II.

A member of the *longicauda* group. General aspect of fish small, flat, and slender, with a long and slender caudal peduncle. Body wider in its anterior part. Head large, short and rounded to slightly triangular in dorsal view. Eye small, orbit round, without notch. Odontodes short, densely covering body, conferring fish a velvety aspect. Snout tip naked.

Mouth elliptic with large upper and lower lips. One buccal papilla. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 45$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle not visible in ventral view. Abdomen naked except for lateral abdominal plates. Four to 8 (modally 6) lateral abdominal plates, plates keeled but not sharp. Twenty-five to 27 (modally 26) plates in median lateral series, plates not coalescing.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than soft rays, slightly curved, reaching beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, reaching beyond anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin truncated with i,12,i rays.

### Colouration

In alcohol, background colour of dorsal surface of head and body variable, from dark brown to reddish brown or light tan, with 5 thick postdorsal dark bands. Anterior part of body darker. Ventral surface lighter, yellowish tan. Fin rays yellowish tan with indistinct dark brown spots more or less forming stripes. Fin membranes hyaline. Caudal fin with indistinct dark stripes (2). Distal caudal-fin margin yellowish.

### Sexual dimorphism

Males with larger head and thickened pectoral spines, bearing hypertrophied odontodes.

### Distribution and habitat

Occurs in mountainous areas in the Lucifer and Galbao massifs in Central French Guiana (Fig. 5). In the Lucifer Mountains, the species has been collected with representatives of *Rivulus igneus* and *Ituglanis* sp.

### Etymology

The species group name *lucifer* refers to the type locality. A name used in apposition.

### *Harttiella longicauda* Covain & Fisch-Muller, new species (Figs 5, 11; Tabs I, II)

#### Holotype

MNHN 2011-0027 (ex MHNG 2699.070 specimen GF07-049), 52.46 mm SL, French Guiana, Trinité Mountains, Mana River drainage, in a tributary of Crique Baboune, Crique Aya around 100m in front of Aya Camp,  $4^{\circ}36'11''\text{N}$ - $53^{\circ}25'04''\text{W}$ , alt. 122 m, Montoya-Burgos and Melki, 28 Nov.-4 Dec. 2007.

#### Paratypes

MNHN 2011-0028 (23, ex MHNG 2699.070); MHNG 2699.070 (23); NZCS F7075 (2, ex MHNG 2699.070); ANSP 190961 (2, ex MHNG 2699.070); MZUSP 108148 (2, ex MHNG 2699.070), same data as holotype. MNHN 2011-0029 (2, ex MHNG 2699.098); MHNG 2699.098 (2), French Guiana, Trinité Mountains, Mana River drainage, in a tributary of Crique Aya at foot of the inselberg,  $4^{\circ}36'33''\text{N}$ - $53^{\circ}24'46''\text{W}$ , alt. 149 m, Montoya-Burgos and Melki, 28 Nov.-4 Dec. 2007. MNHN 2011-0030 (8, ex MHNG 2723.094); MHNG 2723.094 (8), French Guiana, Balenfois Mountains, Approuague River drainage, around 1 km upstream of Nouragues camp, Crique Cascades, Gaucher, Feb. 2008. MHNG 2723.095 (1, ex MHNG 2643.030), French Guiana, Sinnamary River drainage, at mouth of Crique Coeur Maroni, Le Bail *et al.*, 15 Oct. 1982 or 2 Feb. 1983.

### Diagnosis

*Harttiella longicauda* is distinguished from all other congeneric species except *H. pilosa* by the frequent presence of few small preanal plates (vs no preanal plates), and by its specific barcode sequences (JF292277, JF292278, JF292279, JF292280, JF292282, JF292283). It can be distinguished from *H. pilosa* by having the pectoral girdle wider than pelvic girdle (vs pectoral girdle approximately as wide as the pelvic girdle). Additionally six unique morphometric variables distinguish *H. longicauda* from all other conge-



Figure 9. - *Harttiella intermedia*, holotype, MNHN 2011-0021, 34.67 mm SL, French Guiana, Sinnamary River drainage, Tabular Mountain of Trinité massif, Crique Grand Leblond.

ners (Tab. V). *Harttiella longicauda* possesses shorter pelvic spines [mean =  $19.36 \pm 1.17\%$  of SL vs  $20.55 \pm 0.36 < \text{mean} < 24.67 \pm 1.46\%$  of SL; (HSD, p-values  $< 0.0045$ )]; a smaller body width at eighth postdorsal plate [mean =  $9.29 \pm 1.07\%$  of SL vs  $10.28 \pm .98 < \text{mean} < 11.48 \pm 0.94\%$  of SL; (HSD, p-values  $< 0.0238$ )], body width at fourteenth postdorsal plate [mean =  $3.99 \pm 0.51\%$  of SL vs  $4.72 \pm 0.62 < \text{mean} < 5.59 \pm 0.70\%$  of SL; (HSD, p-values  $< 0.0198$ )], minimum caudal peduncle depth [mean =  $2.53 \pm 0.18\%$  of SL vs  $3.24 \pm 0.21 < \text{mean} < 4.86 \pm 0.43\%$  of SL; (HSD, p-values  $< 0.0001$ )], interorbital width [mean =  $33.82 \pm 2.03\%$  of HL vs  $35.25 \pm 1.21 < \text{mean} < 38.20 \pm 2.03\%$  of HL; (HSD, p-values  $< 0.03$ )], and head depth at internostril [mean =  $33.19 \pm 1.76\%$  of HL vs  $33.89 \pm 2.22 < \text{mean} < 36.74 \pm 4.00\%$  of HL; (HSD, p-values  $< 0.0083$ )].

#### Description

Morphometric and meristic data in table I, and GenBank accession numbers in table II.

General aspect of fish small, flat, and slender, with a long and slender caudal peduncle. Body wider in its anterior part. Head large, short and rounded in dorsal view. Eye small, orbit round, without notch. Odontodes short, densely covering body, conferring fish a velvety aspect. Snout tip naked.

Mouth elliptic with large upper and lower lips. One buccal papilla. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 45$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle not visible in ventral view. Abdomen naked except for few rhombic preanal plates, and lateral plates.





Figure 10. - *Harttiella lucifer*, holotype, MNHN 2011-0023, 42.68 mm SL, French Guiana, Mana River drainage, Lucifer Mountains, West of Crique Cascade.

Five to 8 (modally 6) lateral abdominal plates. Twenty-five to 27 (modally 26) plates in median lateral series, plates not coalescing.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than branched rays, slightly curved, reaching pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, reaching anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin truncated with i,12,i rays.

#### Colouration

In alcohol, background colour of dorsal surface of head and body variable, from dark brown tan to greyish tan, with 5 thick postdorsal dark bands. Anterior part of body darker.

Population from Crique Cascade, Approuague River drainage, with dark spots or vermiculations on head. Ventral surface lighter, yellowish tan. Often with a dark blotch at anal-fin origin. Fin rays yellowish tan with indistinct dark brown spots more or less forming stripes. Fins membranes hyaline. Caudal fin with indistinct, poorly defined, dark stripes.

#### Sexual dimorphism

Males with a wider head and thickened pectoral spines bearing hypertrophied odontodes.

#### Distribution and habitat

Occurs in mountainous areas in the Trinité and Balenfois massifs in Northern French Guiana (Fig. 5). In the Trinité





Figure 11. - *Harttiella longicauda*, holotype, MNHN 2011-0027, 52.46 mm SL, French Guiana, Trinité Mountains, Mana River drainage, in a tributary of Crique Baboune, Crique Aya around 100 m in front of Aya Camp.

Mountains, the species has been collected with representatives of *Guyanancistrus* aff. *brevispinis*, *Krobia itanyi*, *Rhamdia quelen*, *Ancistrus* cf. *leucostictus*, *Lithoxus planquettei*, *Characidium fasciadorsale*, *Melanocharacidium* cf. *dispilomma*, and *Rineloricaria* aff. *stewarti*.

#### Etymology

The species group name *longicauda* is from Latin *longus* meaning long, and *cauda* meaning tail. The name makes reference to the shape of the caudal peduncle.

#### *Harttiella janmoli* Covain & Fisch-Muller, new species (Figs 5, 12; Tabs I, II)

##### Holotype

MNHN 2011-0031 (ex MHNG 2695.059), 47.13 mm SL, French Guiana, Maroni River drainage, Kotika Mountain, 3°57'16"N-54°10'50"W, alt. 515 m., Tostain, 5 Sept. 2007.

##### Paratypes

MNHN 2011-0032 (35, ex MHNG 2695.059); MHNG 2695.059 (36); NZCS F7076 (2, ex MHNG 2695.059);

ANSP 190962 (2, ex MHNG 2695.059); MZUSP 108149 (2, ex MHNG 2695.059); RMNH.PISC.37459 (1, ex MHNG 2695.059); RMNH.PISC.37460 (1, ex MHNG 2695.059), same data as holotype.

### Diagnosis

*Harttiella janmoli* is distinguished from all other congeneric species by its dark brown colouration with a large transverse postdorsal saddle corresponding to the position in congeners of the third and fourth bands posterior to dorsal-fin origin (vs brownish colouration normally with five postdorsal bands). Additionally 10 morphometric variables strictly characterize *H. janmoli* (Tab. V). *Harttiella janmoli* possesses longer pectoral spines [mean =  $27.14 \pm 1.54\%$  of SL vs  $21.14 \pm 0.98 < \text{mean} < 24.06 \pm 0.84\%$  of SL; (HSD, p-values < 0.0001)], pelvic spines [mean =  $24.67 \pm 1.46\%$  of SL vs  $19.36 \pm 1.17 < \text{mean} < 22.86 \pm 1.64\%$  of SL; (HSD, p-values < 0.0001)]; a greater anus to pelvic-fin origin length [mean =  $12.88 \pm 0.96\%$  of SL vs  $9.29 \pm 1.42 < \text{mean} < 11.31 \pm 1.01\%$  of SL; (HSD, p-values < 0.012)], anus to pectoral-fin origin length [mean =  $34.24 \pm 1.67\%$  of SL vs  $28.38 \pm 2.75 < \text{mean} < 31.85 \pm 2.26\%$  of SL; (HSD, p-values < 0.0001)], and anus to tip of snout length (mean =  $49.81 \pm 1.63\%$  of SL vs  $43.32 \pm 1.42 < \text{mean} < 48.09 \pm 1.93\%$  of SL; (HSD, p-values < 0.0002)]; a wider body at dorsal-fin origin [mean =  $23.46 \pm 1.18\%$  of SL vs  $17.28 \pm 1.11 < \text{mean} < 20.06 \pm 1.61\%$  of SL; (HSD, p-values < 0.0001)]; and a deeper body at dorsal-fin origin [mean =  $14.80 \pm 1.14\%$  of SL vs  $9.86 \pm 0.79 < \text{mean} < 11.41 \pm 1.41\%$  of SL; (HSD, p-values < 0.015)].

### Description

Morphometric and meristic data in table I.

A representative of the *crassicauda* group. General aspect of fish small and stocky, with a short, large, thick and flattened caudal peduncle. Head large, short and rounded in dorsal view. Eye small, orbit round, without notch. Odontodes short, densely covering body, conferring fish a velvety aspect. Snout tip naked.

Mouth elliptic with large and thick upper and lower lips. One buccal papilla. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth not numerous ( $\approx 30$  per jaw), pedunculated and arranged in a single, comblike row. Subpreopercle not visible in ventral view. Abdomen naked except for lateral abdominal plates. Five to 8 (modally 7) lateral abdominal plates. Twenty-four to 26 (modally 25) plates in median lateral series, plates not coalescing.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than branched rays, slightly curved to S-shaped, reaching beyond pelvic-fin origin. Pelvic fin with i,5 rays;

spine longer, reaching beyond anal-fin origin. Anal fin with i,4 rays, spine longer. Caudal fin truncated with i,12,i rays.

### Colouration

In alcohol, background colour of dorsal surface of head and body dark brown, with usually 4 thick postdorsal dark bands, bands in the position of the third and fourth of congeners merged into a large black transverse saddle on the caudal peduncle. Anterior part of body darker, almost black in certain areas. Ventral surface lighter, yellowish tan. Often with a dark blotch at anal-fin origin. Fin rays yellowish tan with indistinct dark brown spots more or less forming stripes. Fins membranes hyaline, becoming lighter toward distal margins. Caudal fin with poorly defined dark stripes. Medial part of caudal fin with a lighter yellowish band.

### Sexual dimorphism

Males with a wider head and thickened pectoral spines bearing hypertrophied odontodes. Body more densely covered by odontodes than in females, especially on head.

### Distribution and habitat

Only known from type locality in French Guiana, in a small forest creek of the Kotika Mountains at an altitude of 515 m (Fig. 5).

### Etymology

The species group name *janmoli* honours the Dutch ecologist Jan H. Mol for his strong personal investment in the knowledge and protection of *Harttiella*, especially in Suriname where he recovered the highly vulnerable *H. crassicauda*.

### *Harttia* Steindachner, 1877

*Harttia* Steindachner, 1877: 668. Type species: *Harttia loricariformis* Steindachner, 1877. Type by monotypy. Gender: Feminine.

*Harttia* is significantly distinguished from all other Guianese Harttiini by 29 morphometric variables (Tab. V) among which, six possessed very strong loadings onto PCA axes (Fig. 1b). *Harttia* is diagnosed from other Guianese Harttiini by a wider body at anal-fin origin [mean =  $14.98 \pm 1.44\%$  of SL vs  $13.50 \pm 1.43$  (HSD, p-value < 0.0001) and  $12.02 \pm 1.03$  (HSD, p-value < 0.0001) in *Harttiella* and *Cteniloricaria*, respectively], at eighth postdorsal plate [mean =  $12.28 \pm 1.50\%$  of SL vs  $10.59 \pm 1.29$  (HSD, p-value < 0.0001) and  $9.30 \pm 0.95$  (HSD, p-value < 0.0001) in *Harttiella* and *Cteniloricaria*, respectively], and at fourteenth postdorsal plate [mean =  $5.27 \pm 0.81\%$  of SL vs  $4.76 \pm 0.77$  (HSD, p-value < 0.0001) and  $3.96 \pm 0.46$  (HSD, p-value < 0.0001) in *Harttiella* and *Cteniloricaria*, respectively]; a greater nostril to tip of snout length [mean =  $42.45 \pm 2.47\%$  of HL vs  $41.74 \pm 2.23$  (HSD, p-val-



Figure 12. - *Harttiella janmoli*, holotype MNHN 2011-0031, 47.13 mm SL, French Guiana, Maroni River drainage, Kotika Mountain.

ue < 0.0001) and  $38.98 \pm 2.71$  (HSD, p-value < 0.0001) in *Harttiella* and *Cteniloricaria*, respectively]; and more numerous premaxillary [mean =  $80 \pm 17$  vs  $34 \pm 8$  (HSD, p-value < 0.0001) and  $40 \pm 12$  (HSD, p-value < 0.0001) in *Harttiella* and *Cteniloricaria*, respectively] and dentary teeth [mean =  $78 \pm 17$  vs  $33 \pm 8$  (HSD, p-value < 0.0001) and  $39 \pm 10$  (HSD, p-value < 0.0001) in *Harttiella* and *Cteniloricaria*, respectively]. The following combination of characters also differentiates the genus: abdomen partially to wholly covered by very small, rhombic, plates without particular organization. Abdominal plating sometimes restricted to preanal and lateral abdominal plates. Body large, flattened covered by very short odontodes conferring a rather smooth aspect to the species. Subpreopercle exposed. Lateral plates keeled and coalescing toward the end of caudal peduncle. Caudal peduncle becoming more compressed between the eighth and fourteenth postdorsal plates.

Within the *Harttia* group, very strong morphological structures were found with significant differences in PCA scores on the two first axes ( $\chi^2_{K-W} = 128.9601$ , p-val-

ue < 0.0001;  $\chi^2_{K-W} = 44.2382$ , p-value < 0.0001). Deep genetic divergences were also recovered with K2P distances ranging between 0 and 0.19. Considering the different populations of *H. guianensis*, slight differences in shape were found on axis 1 ( $\chi^2_{K-W} = 35.4856$ , p-value < 0.0001;  $\chi^2_{K-W} = 0.1685$ , p-value = 0.9192), and almost no differences in genetics ( $0 < K2P < 0.0017$ ). The three populations of *H. guianensis* (Maroni, Sinnamary, and Approuague drainages) therefore correspond to a single, morphologically relatively plastic, species. Significant differences between populations were highlighted and characterized in Covain *et al.* (2006), and are not repeated herein. Significant differences in shape were also recorded between *H. surinamensis* and the populations from Coppename and Paru de Oeste Rivers ( $\chi^2_{K-W} = 17.9322$ , p-value = 0.0001;  $\chi^2_{K-W} = 14.1004$ , p-value = 0.0009), whereas slight genetic differences of populational level were obtained between *H. surinamensis* and the population from Coppename River (K2P = 0.012), and deep divergences of between species level between *H. surinamensis* and the population of Paru de Oeste River



(K2P = 0.07). Nevertheless no morphometric differences were found between Coppename and Paru de Oeste populations ( $W = 358$ ,  $p$ -value = 0.5305;  $W = 280$ ,  $p$ -value = 0.415), even though these two populations diverged from a K2P distance of 0.068. Moreover, significant differences in shape were recovered by both axes between *H. surinamensis* and the population of Coppename River on one hand ( $W = 1138$ ,  $p$ -value = 0.0027;  $W = 1175$ ,  $p$ -value = 0.0008), and the population of Paru de Oeste on the other hand ( $W = 1344$ ,  $p$ -value = 0.0002;  $W = 1209$ ,  $p$ -value = 0.0111). These three populations represent distinct species, with the one from Coppename River sharing the morphology of the species from Paru de Oeste, and possessing a mitochondrial signal close to the one of *H. surinamensis*. *Harttia fowleri* does not possess strong morphometric differences compared to other *Harttia* ( $W = 2002$ ,  $p$ -value = 0.9877;  $W = 2498$ ,  $p$ -value = 0.0298). Nevertheless, it possesses the strongest genetic divergences, with K2P distances ranging between 0.176 and 0.190.

### ***Harttia guianensis* Rapp Py-Daniel & Oliveira, 2001**

(Supplementary material S5)

*Harttia guianensis* Rapp Py-Daniel & Oliveira, 2001: 88, Fig. 6. Type locality: Approuague River, Saut Athanase, 4°11'N-52°19'W, French Guiana. Holotype: MNHN 1998-0395.

*Harttia guianensis* Rapp Py-Daniel & Oliveira, 2001: Isbrücker, 2001: 27; Isbrücker, 2002: 16; Ferraris in Reis *et al.*, 2003: 335; Provenzano *et al.*, 2005: 521; Covain *et al.*, 2006: 9; Ferraris, 2007: 241; Vari *et al.*, 2009: 29.

*Harttia surinamensis* not Boeseman, 1971: Boujard *et al.*, 1997: 141; Le Bail *et al.*, 2000: 274.

Morphometric and meristic data are provided in table I, and GenBank accession numbers for barcodes in Table II. *Harttia guianensis* is distinguished from congeneric species by five morphometric variables (Tab. V). *Harttia guianensis* possesses a longer caudal peduncle [mean =  $48.73 \pm 1.29\%$  of SL vs  $46.54 \pm 1.17 < \text{mean} < 47.67 \pm 1.04\%$  of SL; (HSD,  $p$ -values < 0.0002)]; a smaller anus to tip of snout length [mean =  $39.60 \pm 1.15\%$  of SL vs  $40.74 \pm 0.70 < \text{mean} < 41.84 \pm 1.02\%$  of SL; (HSD,  $p$ -values < 0.0001)]; a shorter snout [mean =  $54.51 \pm 2.03\%$  of HL vs  $56.52 \pm 2.01 < \text{mean} < 58.89 \pm 5.12\%$  of HL; (HSD,  $p$ -values < 0.0001)]; and a smaller nostril to tip of snout length [mean =  $41.04 \pm 1.85\%$  of HL vs  $42.42 \pm 2.21 < \text{mean} < 43.94 \pm 1.69\%$  of HL; (HSD,  $p$ -values < 0.0003)], and head depth [mean =  $35.27 \pm 2.23\%$  of HL vs  $36.52 \pm 1.80 < \text{mean} < 39.75 \pm 2.37\%$  of HL; (HSD,  $p$ -values < 0.0254)]. K2P distances to congeneric species ranged from 0.064 to 0.183 according to the population. Its colouration confers it camouflage with rocks in its natural habitat, making it difficult to observe (Supplementary material S6-A). The background colour of the dorsal surface is yellowish tan to beige. A dark, almost black, marbling covers the dorsal surface and five black postdorsal bands are present. In juveniles, this pattern exhibits greater contrast

and the head appears greenish with a golden area on the supra-occipital and between the eyes; eye copper coloured. A large black basicaudal blotch is present. The caudal fin is deeply forked and has the distal ends of upper and lower lobes black, and the medial part bright yellow. A black blotch is also often present on the tip of the dorsal fin. All paired fins and dorsal fin possess dark spots on rays forming distinct stripes. The lower surface is yellowish tan. The abdominal plating is restricted to lateral abdominal plates (5 to 8, modally 7) and to the preanal plates. Two large quadrangular plates are present immediately in front of the anus and are bordered by smaller plates up to the pelvic-fin insertion. *Harttia guianensis* has usually 29 plates in the lateral series, these plates are keeled and coalescing toward the 20<sup>th</sup> to 22<sup>nd</sup> plates. The caudal peduncle becomes much more compressed after the confluence of plates. The head is large, with a large elliptic mouth with papillose lips. The subpreopercle is well exposed, triangular, and covered by odontodes. The teeth are numerous (around 80 on each jaw), pedunculated, and arranged in two staggered, comblike rows. In males, the sexual dimorphism consists in the hypertrophy of odontodes on the upper surface of the thickened pectoral spines, on the snout margin, and on keels of the lateral plates. The sexual dimorphism is seasonal. Evers and Seidel (2005) reported that breeding males lost the hypertrophied odontodes of the pectoral spines, at least five days after breeding. This species occurs in coastal drainages of French Guiana and Suriname, from the Approuague River to the Maroni/Marowijn River (Fig. 5). It is an inhabitant of the main channel of rivers, where it colonizes rocky and sandy areas in fast flowing waters. The species is locally very abundant, and is often syntopic with *C. platystoma*, except in Approuague River.

### ***Harttia surinamensis* Boeseman, 1971**

(Supplementary material S7)

*Harttia surinamensis* Boeseman, 1971: 28, pl. 3. Type locality: Grandam, Gran Rio, upper Suriname River, Suriname. Holotype: RMNH 26388 (188.30 mm specimen, holotype not separated from paratypes).

*Harttia surinamensis* Boeseman, 1971: Isbrücker, 1980: 90; Burgess, 1989: 439; Langeani *et al.*, 2001: 141; Rapp Py-Daniel and Oliveira, 2001: 80; Isbrücker, 2001: 27; Isbrücker, 2002: 16; Ferraris in Reis *et al.*, 2003: 335; Provenzano *et al.*, 2005: 521; Covain *et al.*, 2006: 9; Ferraris, 2007: 242; Vari *et al.*, 2009: 39.

Morphometric and meristic data are provided in table I, and GenBank accession number for barcode in table II. Two morphometric variables strictly characterized *H. surinamensis* (Tab. V). *Harttia surinamensis* is distinguished from all congeneric species except *H. tuna* n. sp. by a longer head (shorter compared to *H. tuna*) [mean =  $24.15 \pm 1.38\%$  of SL vs  $23.19 \pm 1.33 < \text{mean} < 23.45 \pm 0.95\%$  of SL; (HSD,  $p$ -values < 0.0364), and mean =  $24.97 \pm 1.14\%$  of SL in *H. tuna* (HSD,  $p$ -value = 0.0033)]; a wider body at eighth

postdorsal plate compared to *H. guianensis* and *H. fowleri* [mean =  $12.35 \pm 1.63\%$  of SL vs  $11.69 \pm 1.32 < \text{mean} < 11.82 \pm 1.25\%$  of SL; (HSD,  $0.0113 < p\text{-values} < 0.0325$ )], and narrower compared to *H. tuna* and *H. fluminensis* n. sp. [mean =  $12.35 \pm 1.63\%$  of SL vs  $13.28 \pm 1.47 < \text{mean} < 13.52 \pm 0.97\%$  of SL; (HSD,  $0.001 < p\text{-values} < 0.007$ )]. K2P distances to congeneric species ranged between 0.064 and 0.176. Its colouration is reminiscent of the substrate, making it difficult to observe in its natural habitat (Supplementary material S6-B). The background colour of the dorsal surface is yellowish tan. Dark marbling covers the dorsal surface and five indistinct postdorsal bands are present, the last three toward the tail being more clearly marked. The eyes are copper coloured. A large deep-black band covers the basal one third of the caudal-fin surface. The caudal fin is deeply forked with the distal end of the lower lobe black, and the medial part bright yellow. A blackish thin band is present in the yellow part of the caudal fin. A black blotch is also often present on the tip of the dorsal fin. All paired fins and dorsal fin possess dark spots on the rays forming distinct stripes. The lower surface is yellowish tan. The abdominal plating is complete in specimens  $> 150$  mm SL, but otherwise usually incomplete, and made of small granular platelets without particular organization. Ontogenetic development of the abdominal cover starts with the appearance (around 80 mm SL) of small granular platelets at the border of the preanal plates. The number of platelets increases then slowly with fish size, until establishing a connection between the preanal plates and the lateral abdominal plates (around 90 mm SL). The number of platelets then continues to increase in the preanal area, along the pelvic-fin insertion, and along the lateral abdominal plates. When the region delimited by the preanal plates, and the pelvic-fin insertion is almost wholly plated, a second transverse arch of platelets crosses the abdomen starting from the insertion of pelvic spines, or the first lateral abdominal plates (around 110 mm SL). The transverse arch becomes thicker with the increasing number of platelets. The region between the arch and the preanal area is eventually covered, and a medial row of platelets appears on the abdomen (around 140 mm SL). The number of platelets along the lateral abdominal plates continues to increase with the size of the fish, as well as in the middle part of the abdomen, making the medial row thicker. The regions delimited by the medial row, and the left and right series of lateral abdominal plates are then little by little covered by platelets, and the convergence is obtained around 180 mm SL. A stage of this developmental pattern is present in almost all specimens of *H. surinamensis*, but the size to which the abdomen appears wholly plated is highly variable among individuals. *Harttia surinamensis* has usually 29 plates in the lateral series, these plates keeled and coalescing toward the 19<sup>th</sup> to 22<sup>nd</sup> plates. The caudal peduncle becomes abruptly more compressed after the confluence of plates. The head is large, with a large elliptic mouth with

papillose lips. The subpreopercle is well exposed, triangular, and covered by odontodes. The teeth are numerous (approximately 80 on each jaw), pedunculated, and arranged in two staggered, comblike rows. Sexual dimorphism consists of the hypertrophy of odontodes on the upper surface of the thickened pectoral spines in mature males. *Harttia surinamensis* is restricted to the Suriname River (Fig. 5) where it frequents the main channel over rocky and sandy bottoms, in fast flowing waters. The species is locally very abundant, and is often syntopic with *C. platystoma*.

***Harttia fluminensis* Covain & Fisch-Muller, new species**  
(Figs 5, 13; Tabs I, II)

*Holotype*

MHNG 2724.003 (ex MHNG 2690.013, specimen SU01-458), 151.14 mm SL, Suriname, Coppename River at Raleighvallen, Mol, 30 Nov. 2006.

*Paratypes*

MHNG 2690.013 (14); MNHN 2011-0033 (2, ex MHNG 2690.013); same data as holotype. MHNG 2690.012 (6); NZCS F7077 (1, ex MHNG 2690.012), Suriname, Coppename River at Raleighvallen, Mol, 29 Nov. 2006.

*Diagnosis*

*Harttia fluminensis* is distinguished from all congeners except *H. tuna* n. sp. and *H. trombetensis* by an incomplete abdominal cover, restricted to preanal and abdominal lateral plates with a row of platelets joining these two series of plates (vs no row of platelets making junction between preanal and lateral abdominal plates), and by its specific barcode sequence (JF292263). It can be distinguished from *H. tuna* by a deeper head [ $37.31\text{--}43.30$ , mean  $38.94 \pm 1.42\%$  of HL, vs  $31.96\text{--}38.77$ , mean  $36.52 \pm 1.80\%$  of HL (HSD,  $p\text{-value} < 0.0001$ )], and from *H. trombetensis* by colour pattern of caudal fin (a large dark band at base of caudal fin, vs a dark rounded blotch). Additionally *H. fluminensis* is distinguished from all other congeneric species by two morphometric variables (Tab. V). *Harttia fluminensis* possesses a greater minimum caudal peduncle depth [mean =  $1.60 \pm 0.11\%$  of SL vs  $1.35 \pm 0.13 < \text{mean} < 1.43 \pm 0.11\%$  of SL; (HSD,  $p\text{-values} < 0.0001$ )]; and a greater interorbital width [mean =  $24.25 \pm 1.02\%$  of HL vs  $22.04 \pm 1.27 < \text{mean} < 23.12 \pm 1.11\%$  of HL; (HSD,  $p\text{-values} < 0.028$ )].

*Description*

Morphometric and meristic data in table I, and GenBank accession numbers in table II.

General aspect of fish flat and broad, with a thick caudal peduncle before confluence of lateral keels. Head large, short and triangular to slightly rounded in dorsal view. Eye large, orbit more or less round, without notch. Odontodes



very short, conferring fish a smooth aspect. Snout tip naked.

Mouth elliptic with large and thick upper and lower lips. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 90$  per jaw), pedunculated and arranged in two staggered, comblike rows. One buccal papilla. Subpreopercle well exposed in ventral view, triangular, and covered by odontodes. Abdomen naked except for preanal plates, lateral abdominal plates, and a row of platelets making junction between previous series of plates. Six to 9 (modally 7) lateral abdominal plates, plates keeled but not sharp. Two large preanal plates. Twenty-nine to 30 (modally 29) plates in median lateral series. Lateral plates keeled, coalescing between 7<sup>th</sup> and 9<sup>th</sup> last postdorsal plates. Caudal peduncle abruptly compressed after confluence of lateral plates.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than soft rays, slightly curved, reaching much beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, just reaching anal-fin origin. Anal fin with i,4 rays, spine shorter. Caudal fin forked with i,12,i rays.

#### Colouration

In alcohol, background colour of dorsal surface of head and body dark brown tan, with 5 to 6 indistinct postdorsal dark bands and dark marbling. Ventral surface lighter, yellowish tan. Abdomen whitish. A large dark band at base of caudal fin representing 1/3 of the fin surface. Distal two-thirds of caudal fin lighter with a thinner dark band. Tip of lower lobe black. Fin rays yellowish tan with distinct dark brown spots forming stripes. Tip of dorsal fin with a black blotch. Fins membranes hyaline, except paired fins reddish anteriorly.

#### Sexual dimorphism

Males with a wider head and thickened pectoral spines bearing hypertrophied odontodes.

#### Distribution and habitat

Only known from the Coppename River drainage in Suriname (Fig. 5), where it frequents the main channel over rocky and sandy bottom, in fast flowing waters.

#### Etymology

The species group name *fluminensis* is from Latin *flumen* meaning river, and makes reference to the ecology of *Harttia* that represents a group of rheophilic fish from the main channel of rivers.

***Harttia tuna* Covain & Fisch-Muller, new species** (Figs 5, 14; Tabs I, II)

#### Holotype

MZUSP 108150 (ex MHNG 2704.029, specimen SU07-660), 170.95 mm SL, Sipaliwini Savannah in Trio Amerindian territory at the Suriname-Brazil border, Four Brothers Mountains in a tributary of the Paru de Oeste River, gift of the Trio tribe in Sipaliwini, 20-21 Oct. 2007.

#### Paratypes

MHNG 2704.029 (20); MZUSP 108151 (2, ex MHNG 2704.029); MNHN 2011-0034 (2, ex MHNG 2704.029); NZCS F7078 (2, ex MHNG 2704.029), same data as holotype.

#### Diagnosis

*Harttia tuna* is distinguished from all other congeneric species except *H. fluminensis* and *H. trombetensis* by an incomplete abdominal cover restricted to preanal and abdominal lateral plates with a row of platelets joining these two series of plates (vs no row of platelets making junction between preanal and lateral abdominal plates), and by its specific barcode sequence (JF292262). It can be distinguished from *H. fluminensis* by a shallower head [ $31.96\text{--}38.77$ , mean  $36.52 \pm 1.80\%$  of HL, vs  $37.31\text{--}43.30$ , mean  $38.94 \pm 1.42\%$  of HL; (HSD, p-value < 0.0001)], and from *H. trombetensis* by the colour pattern of the caudal fin (a dark rounded blotch at base of caudal fin, vs a large dark band). Four morphometric variables strictly characterize *H. tuna* (Tab. V). *Harttia tuna* possesses a longer head [mean =  $24.97 \pm 1.14\%$  of SL vs  $23.19 \pm 1.33 < \text{mean} < 24.15 \pm 1.38\%$  of SL; (HSD, p-values < 0.0032)]; a greater predorsal length [mean =  $33.58 \pm 0.84\%$  of SL vs  $32.10 \pm 1.05 < \text{mean} < 33.01 \pm 1.11\%$  of SL; (HSD, p-values < 0.017)]; a smaller postdorsal length [mean =  $55.44 \pm 1.10\%$  of SL vs  $56.63 \pm 0.94 < \text{mean} < 57.35 \pm 1.26\%$  of SL; (HSD, p-values < 0.0157)]; and a smaller orbital diameter [mean =  $20.97 \pm 1.12\%$  of HL vs  $22.68 \pm 1.43 < \text{mean} < 23.37 \pm 1.08\%$  of HL; (HSD, p-values < 0.0006)].

#### Description

Morphometric and meristic data in table I, and GenBank accession number in table II.

General aspect of fish flat and broad, with a thick caudal peduncle before confluence of lateral keels. Head large, short and triangular to slightly rounded in dorsal view. Eye large, orbit more or less round, without notch. Odontodes very short, conferring fish a smooth aspect. Snout tip naked.

Mouth elliptic with large and thick upper and lower lips. Surface of lips papillose, with numerous papillae. Distal margin of the lower lip fringed with minute triangular papillae. Maxillary barbel minute. Teeth numerous ( $\approx 90$  per jaw),



Figure 13. - *Harttia fluminensis*, holotype, MHNG 2724.003, 151.14 mm SL, Suriname, Coppename River at Raleighvallen.

pedunculated and arranged in two staggered, comblike rows. One buccal papilla. Subpreopercle well exposed in ventral view, triangular, and covered by odontodes. Abdomen naked except for preanal plates, lateral abdominal plates, and a row of platelets making junction between previous series of plates. Six to 9 (modally 7) lateral abdominal plates, plates keeled but not sharp. Two medium sized preanal plates. Twenty-nine to 30 (modally 29) plates in median lateral series. Lateral plates keeled, coalescing between 7<sup>th</sup> and 9<sup>th</sup>

last postdorsal plates. Caudal peduncle abruptly compressed after confluence of lateral plates.

Dorsal-fin origin more or less in front of pelvic-fin insertion. Dorsal and pectoral fins with i,6 rays. Pectoral spine longer than branched rays, slightly curved, reaching much beyond pelvic-fin origin. Pelvic fin with i,5 rays; spine longer, just reaching anal-fin origin. Anal fin with i,4 rays, spine shorter. Caudal fin forked with i,12,i rays.

### Colouration

In alcohol, background colour of dorsal surface of head and body greyish tan, with 6 to 7 indistinct postdorsal darker bands and brownish poorly defined spots and marbling. A large black quadrangular area below eyes. Ventral surface lighter, yellowish. Abdomen whitish. A large dark band at base of caudal fin representing 1/3 of fin surface. External part of caudal fin lighter with a thinner brownish band. Tip of lower lobe black. Fin rays yellowish tan with distinct dark brown spots forming stripes. Tip of dorsal fin with a black blotch. Fins membranes hyaline.

### Sexual dimorphism

Males with a larger head and thickened pectoral spines bearing hypertrophied odontodes.

### Distribution and habitat

Known from upper Paru de Oeste River (Fig. 5).

### Etymology

The species group name *tuna* is from the Amerindian Trio-Wayana meaning river, water. It refers to *H. fluminensis*, which has a name with the same meaning, because of their extreme morphological resemblance. A name used in apposition.

### *Harttia fowleri* (Pellegrin, 1908)

(Supplementary material S8)

*Oxyloricaria fowleri* Pellegrin, 1908: 126. Type locality: Rivière Camopi (Guyane française). Holotype: MNHN 1901-0372.

*Harttia fowleri* (Pellegrin, 1908): Boeseman, 1971: 9; Rapp Py-Daniel and Oliveira, 2001: 81; Provenzano *et al.*, 2005: 21; Covain *et al.*, 2006: 9.

*Cteniloricaria fowleri* (Pellegrin, 1908): Isbrücker, 1979: 91; Burgess, 1989: 440; Le Bail *et al.*, 2000: 266; Isbrücker, 2001: 26, 30; Isbrücker, 2002: 15; Ferraris *in* Reis *et al.*, 2003: 331; Ferraris, 2007: 233; Vari *et al.*, 2009: 39.

Morphometric and meristic data are provided in table I, and GenBank accession number for barcode in table II. Only one morphometric variable distinguishes *H. fowleri* from all congeneric species (Tab. V). *Harttia fowleri* possesses more numerous lateral abdominal plates [mean =  $10 \pm 2$  vs  $7 \pm 1 < \text{mean} < 8 \pm 2$ ; (HSD, p-values < 0.0001)]. K2P distances to congeneric species ranged between 0.176 and 0.190. Its colouration mimics the substrate. The background colour of the dorsal surface is reddish tan (Supplementary material S6-C). Sparse dark marbling covers the head surface and 5 to 8 (modally 6) distinct postdorsal bands are present. The eyes are golden to copper-coloured. In juveniles, this colour pattern is more contrasted over a rather greenish background dorsal colour (Supplementary material S6-D). A large deep black basicaudal blotch is present. The caudal fin is deeply forked with the distal end of the

lower and upper lobes black, and the medial part yellowish. A black blotch is also present on the tip of the dorsal fin. All paired-fins and dorsal-fin spines are covered with dark spots. The surface colour of paired fins is reddish anteriorly, rather yellowish further posteriorly, and blackish toward their extremity. The lower surface of body is yellowish tan. The abdominal plating is complete in specimens greater than 120 mm SL, made of small granular platelets without particular organization. Abdominal plating reaches gill opening with the throat not covered, and the anterior margin V-shaped. Ontogenetic development of the abdominal cover is similar to that of *H. surinamensis*, begins at a smaller size and is always complete in adults. *Harttia fowleri* usually has 29 plates in the lateral series, these plates are keeled and coalescing toward the 19<sup>th</sup> to 21<sup>st</sup> plates. The caudal peduncle becomes abruptly more compressed after the confluence of plates. The head is wide, with a large elliptic mouth with papillose lips. The subpreopercle is well exposed, triangular, and covered by odontodes. The teeth are numerous (around 75 on each jaw), pedunculated, and arranged in a single, comblike row. The sexual dimorphism is unknown despite a large sampling effort, but could be reminiscent of what can be observed in other *Harttia*. Some specimens bear thicker pectoral spines with few, well visible odontodes. Moreover, such specimens, suspected to be males, also possess longer pectoral and pelvic-fin spines which are prolonged into soft extensions (not filamentous). This species is restricted to the Oyapock/Oiapoque River drainage in French Guiana and Brazil (Fig. 5). This is the largest species of the group within the Guianas, and specimens greater than to 220mm SL are not unusual. It is an inhabitant of the main channel where it colonizes rocky and sandy areas, in fast flowing waters. The species is locally abundant.

## DISCUSSION

This global assessment of the diversity of Harttiini within the Guianas unambiguously demonstrates that the richness of this group was greatly underestimated until now. No fewer than 9 new taxa are presented here increasing the total number of known species to 14 (more than twice the number previously recorded). The Harttiini show strong morphological trends supporting the validity of three genera: *Harttiella*, *Cteniloricaria* and *Harttia*. This division into three entities was also strongly supported by the COI barcodes, with distinct lineage-specific patterns in GC contents and deep genetic divergences between genera (mean = 0.197 K2P distance). Notably, the high divergences between genera found here are greater than reported elsewhere. Ward *et al.* (2009), in a review about the campaign of DNA barcoding in fishes, reported a mean value of  $0.1619 \pm 0.0004$  for the K2P variation within family (= between genera) based





Figure 14. - *Harttia tuna*, holotype, MZUSP 108150, 113.20 mm SL, Sipaliwini Savannah in Trio Amerindian territory at the Suriname-Brazil border, Four Brothers Mountains in a tributary of the Paru de Oeste River.



on the sequencing of 1,677 specimens belonging to 546 species and 273 genera, most of them representing Australian marine forms. In another study conducted on freshwater fishes from Canada, Hubert *et al.* (2008) reported a between genera variation of  $0.1538 \pm 0.0001$  based on the sequencing of 1,360 specimens belonging to 190 species and 85 genera. Our results relating to between and within species levels perfectly corroborate previous findings, with within species K2P distance variation reaching  $0.0027 \pm 0.0005$  in this study vs  $0.0035 \pm 0.0001$  in Ward *et al.* (2009) and  $0.0027 \pm 0.0001$  in Hubert *et al.* (2008). The within genera divergences reached  $0.0878 \pm 0.0333$  in this study and  $0.0811 \pm 0.0004$  and  $0.0837 \pm 0.0003$  in Ward *et al.* (2009) and Hubert *et al.* (2008), respectively. Contrasting slightly with these results, Valdez-Moreno *et al.* (2009) reported a variation of  $0.1357 \pm 0.0007$  at between genera level, and  $0.051 \pm 0.0008$  and  $0.0045 \pm 0.0001$  at within genera and within species levels respectively, in the COI sequences of freshwater fishes from Mexico and Guatemala (results obtained based on 427 specimens representing 61 species and 36 genera). These authors hypothesised a more recent origin of freshwater fishes compared to their marine counterparts to explain differences with Ward *et al.*'s results. Nevertheless, the hypothesis of a younger origin of freshwater fish species is not supported by our results, nor by the study of Hubert *et al.* (2008). The latter, assuming the hypothesis that the fragmentation of freshwater ecosystems leads to stronger genetic structure among populations and to deeper divergence among haplotypes in freshwater fishes than in marine ones (Ward *et al.* 1994), pointed out that the pattern of variation in distances was strikingly similar between both groups (freshwater and marine fishes). Although they detected geographic structure in their data, they concluded that the higher geographic structure in freshwater fishes was not necessarily reflected in deeper intra and interspecific divergence. They nevertheless admitted that the Canadian freshwater fish fauna could be relatively recent given that most of the rivers and lakes were colonized after the glacial retreat at the end of the Pleistocene. The deep differences between genera and the surprisingly similar levels of variation between and within species observed in our data may thus be explained by the fact that Guianese Harttiini represents an ancient lineage, but its diversification within the Guianas could be relatively recent.

Hebert *et al.* (2004) suggested that divergent specimens could be flagged as putative species if they showed 10-fold the mean intraspecific differentiation for the group under study. Ward (2009) demonstrated that this statement was correct, even though rather conservative especially considering cryptic speciation. Ward (2009) refined the approach of Hebert *et al.* (2004), and based on the analysis of 1,088 species of fish, proposed that specimens with divergences greater than 2% were likely to be different species with a probability

greater than 0.95. This threshold applied to a great majority of our data, since all but two species exhibit interspecific variations greater than 0.027 (10x within species distance here of 0.0027) leading to a distinct barcoding gap between species (Meyer and Paulay, 2005). Only *Harttiella intermedia* shares identical barcode sequences with its congener *H. longicauda*, representing less than 6% of all species assignment. Different explanations have been proposed to explain such phenomena (Hebert *et al.*, 2003; Meyer and Paulay, 2005; Hubert *et al.*, 2008; Ward *et al.*, 2009). Introgressive hybridization and poor taxonomy were often put forward. Nevertheless, Hubert *et al.* (2008) pointed out that the establishment of reciprocal monophyly between two sister taxa was also a function of time, given that fixation of a new coalescent follows the line of descent. When not enough time passed to split sister species, one may obtain a paraphyletic grouping with one species nested within a second one (then the coalescent of the first species is contained within the coalescent of the second) or a polyphyletic grouping, both species sharing the same coalescent (Meyer and Paulay, 2005). *Harttiella intermedia* may consequently represent a vicariant form of the latter resulting from a founder effect. Both species being present within the Sinnamary basin, a small population derived from *H. longicauda* may have been quite recently isolated in the Trinité Massif. Following the example of the East African lacustrine cichlid species flock, evolution of morphology in a small isolated population can occur very quickly, before enough time has passed to genetically differentiate the species. *Harttiella intermedia* could therefore represent rather a very recently emerging species whose morphology evolved very quickly making it perfectly distinct from *H. longicauda*. The second problem with the global threshold used here concerned the lineage including *Harttia surinamensis*. The 2% threshold used does not allow recognition of *H. surinamensis* and *H. fluminensis* as distinct species whereas these two entities are clearly morphologically diagnosable. Conversely, this threshold allowed the discovery of two pairs of cryptic species: *Harttia fluminensis* and *H. tuna*, and *Harttiella lucifer* and *H. longicauda*. These two pairs of species are indeed very difficult to distinguish morphologically but the amount of genetic divergence accumulated by both pairs of species left no doubt about their validity. This case of morphological stasis where the ancestral shape of the group was maintained almost identically in the two species while a significant amount of mutation has accumulated in their respective COI genes, contrasts with the case of *H. intermedia* and *H. longicauda*. A last unexpected result was the amount of divergence observed in *Harttia fowleri*. While it appears morphologically very close to Guianese *Harttia*, it possesses smaller genetic divergences with *Cteniloricaria*. Moreover, the NJ unrooted tree obtained here placed *H. fowleri* outside *Harttia* and *Cteniloricaria* at the base of the tree.

Despite the problems generally encountered in highly diversified lineages, the COI barcode approach has proven to be a relevant and powerful tool to assess the global diversity of Harttiini within the Guianas. Moreover, the significant lineage dependence highlighted in GC content, particularly GC1 and GC3, allows envisaging their use directly in a multivariate framework for explanatory or discrimination purposes.

The unifying structure provided by the multi-table approach including genetics, morphometry, and ecology-distribution establishes the link between all types of data, and provided a graphical output allowing recognition of congruence and incongruence between tables. Unsurprisingly, the morphology and genetics were highly congruent, and few variations were observable on the factorial map, the most unstable species between preliminary representations being *H. fowleri*. On the other hand, ecological and distributional data displayed stronger differences. In all respects, the quality of the obtained consensus allowed a detailed exploration of the data. Indisputably, the greatest advantage of the MCOA is the unification of the different variables contained in the different data set within the same analysis. This allows a graphical exploration of those variables and highlights unrevealed associations between them onto co-inertia axes. Indeed, strong correlations were found between an intraphenotypic component composed of genetics and morphology, and an extraphenotypic component made of ecological and distributional variables. Moreover the tests against phylogenetic dependence, first on MCOA axes and secondarily on all variables, allow the interpretation of these associations in an evolutionary perspective. The evolution of Harttiini within the Guianas was thus shaped by (or oriented toward) adaptations to a definite type of biotope. Indeed, *Cteniloricaria* and *Harttia* are members of the rheophilic fauna inhabiting the main stream of rivers, a biotope strongly exposed to the sunlight. These ecological parameters were tightly linked to morphological adaptations such as an increase in size of the caudal peduncle revealing adaptation toward better abilities for swimming (Watson and Balon, 1984), and to an increase in the number of plates providing further protection in these rocky and turbulent biotopes. The increase in size of the eye may imply that these fish are more active by day (higher temperature of the biotope due to higher exposition to the sunlight), thus representing diurnal loricariids, a family of catfishes usually considered as nocturnal. Moreover, *Harttia* possesses strong tendencies toward having a wider caudal peduncle, making it an even more powerful and more efficient swimmer, as well as having more numerous teeth, thereby increasing its ability to grasp algae that grows over rocks. These strong ecomorphological trends probably enable it to exploit its immediate environment more effectively than *Cteniloricaria*. This probably explains the relative scarcity of the latter when both genera are sympatric. This complex relationship nevertheless deserves further research to better

characterize the ecomorphological trends shaping these two genera. In contrast, *Harttiella* evolved adaptations to mountainous forest creeks, a biotope characterised by its cool temperature due to altitude and probably to tree shade, and its greater conductivity due to the small size of the streams (less water compared to the river) and to the abundant dissolved organic matter issued from the decomposition of the constantly falling dead leaves. These adaptations include dwarfism since all *Harttiella* represent dwarf species of Harttiini, the largest specimen presently known being the holotype of *H. longicauda* (52.46 mm SL), as well as changes in shape. These include a tendency for the species to be rather thick-set with broader, longer and deeper head characteristics, and a shorter, broader and thicker caudal peduncle. The eye is small in *Harttiella*, perhaps due to the abundant forest coverage restricting sunlight or to nocturnal habits. An evolutionary trend was also detected in the longitudinal dispersion of Harttiini, *Harttiella* being rather distributed in the eastern part of the Guianas, and *Cteniloricaria* in the western part. Even though an evolutionary gradient is revealed, the areas of dispersal overlap between the three genera. However, this distribution may reflect the capture effort which has been more intense in eastern Guianas. Excluding *H. fowleri*, restricted to the extreme east of the Guianas, and following a gradient from west to east, *Cteniloricaria* is distributed from the Essequibo to the Sinnamary, *Harttia* from the Coppename to the Approuague, and *Harttiella* from the Maroni to the Approuague. *Harttiella* possesses thus the smallest distribution of all Harttiini within the Guianas, as well as the greatest number of species. This implies very limited distribution for several of its representatives, most of them being distributed in patches, particularly in the Maroni system. All members of the *crassicauda* group are restricted to few or even single creeks of a single mountain, making them highly vulnerable. The small size of populations coupled with a potential absence of gene flow within these species (each genetic signal being unique for the time being along the Maroni River for example) may threaten them with extinction in case of severe damage to their immediate environment. This makes them species of conservation interest for the definition of protected areas, and urgent measures should be taken to protect the species being directly affected by mining activities. Only some members of the *longicauda* group seem to have a wider distribution that includes several river systems.

A last result provided by the MCOA may be noted. The fact that principal coordinates computed from the decomposition of the K2P matrix were highly correlated with the MCOA axes, and that these axes were under phylogenetic dependence, implies that the distance matrix contained a significant amount of phylogenetic signal. Moreover the significance of the test of substitution saturation implies that the COI gene is a good candidate for the reconstruction of a phylogeny of Guianese Harttiini. The NJ K2P distance tree

obtained herein could therefore be very close to the topology reconstructed using robust phylogenetic methods. If the position of *H. fowleri* in the NJ tree corresponds to its phylogenetic position, *Harttia* could represent a paraphyletic assemblage. Since all *Harttiella* and *Cteniloricaria* appear to form monophyletic groups in the present topology, the assignment of Guianese representative of *Harttia* to that genus should be reconsidered. A genetic comparison to the type species, *H. loricariformis* from the Paraíba do Sul River in Southeast Brazil would clear up this uncertainty.

The multi-table approach, initially devoted for the study of ecological patterns, has already proven to be relevant in the study of synchrony in the temporal variability of aquatic communities (Bady *et al.*, 2004), or to the contribution of molecular markers to the structures of populations (Jombart *et al.*, 2006). In this study, the MCOA also revealed its ability to extract the evolutionary trends shaped through time in a tribe of poorly differentiated catfishes. Still rarely used, this type of approach should be considered more widely in an evolutionary framework to provide stronger prerequisites for a correct estimation of the underlying forces driving the evolution of the groups under study.

#### KEY TO THE SPECIES OF GUIANESE HARTTIINI

- 1a.** - Minimum caudal peduncle depth 0.94-1.9% of SL . . . **2**  
**1b.** - Minimum caudal peduncle depth 2.0-5.6% of SL . . .  
 . . . . . *Harttiella* **8**  
**2a.** - Presence of a complete abdominal cover in specimens greater than 70 mm SL made of medium sized rhombic plates; caudal fin with a large median black crescent: . . . . .  
 . . . . . *Cteniloricaria* **3**  
**2b.** - Absence of a complete abdominal cover; when present, abdominal cover restricted to lateral abdominal plates, pre-anal plates or made of small granular platelets, cover not complete in specimens smaller than 120 mm SL; caudal fin often with a black basicaudal blotch . . . . . *Harttia* **4**  
**3a.** - Colour pattern of dorsal surface of body distinctly spotted . . . . . *C. napova* (Paru de Oeste River)  
**3b.** - Colour pattern of dorsal surface of body indistinctly blotched or marbled. . . . .  
 . . . . . *C. platystoma* (Essequibo to Sinnamary Rivers)  
**4a.** - Abdominal cover constituted of small granular platelets on the abdomen . . . . . **5**  
**4b.** - Abdominal cover restricted to preanal and lateral plates; a row of platelets may join these two series . . . . . **6**  
**5a.** - Presence of a large basicaudal spot; teeth arranged in a single row . . . . . *H. fowleri* (Oyapock River)  
**5b.** - Presence of a large basicaudal band; teeth arranged in two staggered rows . . . *H. surinamensis* (Suriname River)

- 6a.** - Presence of small granular platelets between lateral abdominal plates and base of pectoral fins; in adults, presence of a row of platelets joining preanal to lateral abdominal plates . . . . . **7**  
**6b.** - Absence of small granular platelets between lateral abdominal plates and base of pectoral fins; in adults, absence of a row of platelets joining preanal to lateral abdominal plates . . . . . *H. guianensis* (Maroni/Marowijne to Approuague Rivers)  
**7a.** - Head depth representing 37.3-43.3% of HL . . . . .  
 . . . . . *H. fluminensis* (Coppename River)  
**7b.** - Head depth representing 32.0-38.8% of HL . . . . .  
 . . . . . *H. tuna* (Paru de Oeste River)  
**8a.** - Minimum caudal peduncle depth representing 7.3-15.8% of caudal peduncle length . . . *crassicauda* group **9**  
**8b.** - Minimum caudal peduncle depth representing 4.3-8.4% of caudal peduncle length . . . . . *longicauda* group **12**  
**9a.** - Colour pattern of caudal fin distinctly banded . . . . .  
 . . . . . *H. parva* (Atachi Bakka Mt)  
**9b.** - Colour pattern of caudal fin not distinctly banded . . **10**  
**10a.** - Dorsal surface with usually 5 well separated dark bands posterior to dorsal-fin origin . . . . . **11**  
**10b.** - Dorsal surface with usually 4 postdorsal bands, 3<sup>rd</sup> band appearing as a large black transverse saddle. . . . .  
 . . . . . *H. janmoli* (Kotika Mt.)  
**11a.** - Caudal peduncle length more than 40% of SL . . . . .  
 . . . . . *H. intermedia* (Trinité Mt.)  
**11b.** - Caudal peduncle length less than 40% of SL . . . . .  
 . . . . . *H. crassicauda* (Nassau Mt.)  
**12a.** - Hispid appearance of mature males, width of pectoral and pelvic girdles almost equivalent . . . . .  
 . . . . . *H. pilosa* (Tortue Mt.)  
**12b.** - Smooth appearance of mature males, pectoral girdle much wider than pelvic girdle . . . . . **13**  
**13a.** Pelvic spine just reaching anal-fin origin . . . . .  
 . . . . . *H. longicauda*  
**13b.** Pelvic spine reaching beyond anal-fin origin . . . . .  
 . . . . . *H. lucifer*

**Acknowledgments.** - We are grateful to Philippe Keith, Romain Causse and Patrice Pruvost, MNHN; Martien van Oijen and Koos van Egmond, RMNH; Ronald Vonk and Hielke Praagman, ZMA; James MacLaine, BMNH; Mark Sabaj Perez and John Lundberg, ANSP for the loan of type and complementary material and welcome in collections; Philippe Gaucher, CNRS Guyane; Olivier Tostain, Ecobios Cayenne; Régis Vigouroux and Philippe Cerdan, Hydreco Guyane; Michel Jégu and Bernard de Mérona, IRD; François Meunier and Yves Fermon, MNHN; Hélène Pagesy, CNRS; Alexandre Fort, Pedro Hollanda Carvalho, Claude Weber and Alain Merguin, MHNG; Maël Dewynter, ONF Guyane; Frédéric Melki, Biotopos France; Kenneth Wan Tong You, Paramaribo; Paul Ouboter, NZCS; Calvin Bernard, CSBD; Vincent Piron and Colin Niel, Parc de la Guyane; the North Rupununi District Development Board (NRDDB); the Association Arataï; the team of *La Boudeuse*;



and the Iwokrama organization for their field and logistic assistance; the G. and A. Claraz Foundation for their financial support for the missions in Suriname in 2001, 2005, 2007 and 2008, and in French Guiana in 2006 and 2010; the Académie Suisse des Sciences Naturelles (ScNat) for their financial support for the missions in Guyana 2004 and French Guiana 2006; The Constantin Topali Found for their financial contribution to the acquisition of field material for the mission Suriname 2007, and lab material in 2009; André Huser, Sallmann-Fehr AG for the gift of gill nets for the mission in Suriname in 2005 and 2007; the Guyana Environmental Protection Agency, and Ministry of Amerindian affairs; the French Guiana Dren, ONF, and Préfecture; and the Surinamese Ministry of Agriculture, Animal Husbandry and Fisheries for the different necessary authorizations and collecting permits. Part of this project was supported by the Fond National Suisse de la Recherche Scientifique (JIMB 3100A0-104005) and the State of Geneva. The pictures and figures were finalized by Philippe Wagneur and Florence Marteau, MHNG. Preliminary results of this study were presented in 4<sup>e</sup> rencontres de l'ichtyologie en France (RIF), Paris, 2009; the 6<sup>e</sup> symposium national de morphométrie et évolution des formes (SMEF), Montpellier, 2009; and the 13<sup>th</sup> Evolutionary Biology Meeting at Marseilles, 2009 with the financial support of the Société Académique de Genève. John A. Hollier, MHNG, improved language usage and style on the earliest version of the manuscript. This manuscript benefited from useful and constructive comments from Carl J. Ferraris, Portland, Robert D. Ward, CSIRO Marine and Atmospheric Research, and Pierre Sagnes, University of Lyon. This work represents part of the PhD dissertation of the first author, who would particularly acknowledge Denis Duboule, University of Geneva, Sonia Fisch-Muller, MHNG, and Stéphane Dray, University of Lyon for their supervision.

## REFERENCES

- ABOUHEIF E., 1999. - A method to test the assumption of phylogenetic independence in comparative data. *Evol. Ecol. Res.*, 1: 895-909.
- AITCHINSON J., 1986. - The Statistical Analysis of Compositional Data. 416 p. London: Chapman & Hall.
- ALBRECHT G., 1978. - Some comments on the use of ratios. *Syst. Zool.*, 27: 67-71.
- ATCHLEY W.R. & ANDERSON D., 1978. - Ratios and the statistical analysis of biological data. *Syst. Zool.*, 27: 71-78.
- ATCHLEY R., GASKINS C.T. & ANDERSON D., 1976. - Statistical properties of Ratios. I. Empirical results. *Syst. Zool.*, 25: 137-148.
- BADY P., DOLÉDEC S., DUMONT B. & FRUGET J.F., 2004. - Multiple co-inertia analysis: a tool for assessing synchrony in the temporal variability of aquatic communities. *C.R. Biol.*, 327: 29-36.
- BAKKER J.P. & LANJOUW J., 1949. - Indrukken van de natuurwetenschappelijke expeditie naar Suriname 1948-49. *Tijdschr. K. Ned. Aardr. Gen.*, 66: 538-557.
- BENJAMINI Y. & YEKUTIELI D., 2001. - The control of the false discovery rate in multiple testing under dependency. *Ann. Stat.*, 29: 1165-1188.
- BOESEMAN M., 1953. - Scientific results of the Surinam expedition 1948-1949. Part II. Zoology, No. 2. The Fishes (I). *Zool. Med.*, 32: 1-24.
- BOESEMAN M., 1971. - The "comb-toothed" Loricariinae of Surinam, with reflections on the phylogenetic tendencies within the family Loricariidae (Siluriformes, Siluroidei). *Zool. Verh.*, 116: 1-56.
- BOUJARD T., PASCAL M., MEUNIER J.F. & LE BAIL P.-Y. (eds.), 1997. - Poissons de Guyane. Guide écologique de l'Approuague et de la réserve des Nouragues. 219 p. Paris: INRA, Hydrobiologie et Aquaculture.
- BURGESS W.E., 1989. - An atlas of freshwater and marine catfishes. A preliminary survey of catfishes. 784 p. Neptune City: T.F.H. Publications, Inc.
- CAILLIEZ F., 1983. - The analytical solution of the additive constant problem. *Psychometrika*, 48: 305-310.
- CHARIF D. & LOBRY J.R., 2007. - Seqin R 1.0-2: a contributed package to the R project for statistical computing devoted to biological sequences retrieval and analysis. In: Structural Approaches to Sequence Evolution: Molecules, Networks, Populations (Bastolla U., Porto M., Roman H.E. & Vendruscolo M., eds), pp. 207-232. New York: Springer Verlag.
- CHESEL D. & HANAFI M., 1996. - Analyses de la co-inertie de K nuages de points. *Rev. Stat. Appl.*, 44: 35-60.
- CORRUCINI S., 1977. - Correlation properties of Morphometric ratios. *Syst. Zool.*, 26: 211-214.
- COVAIN R. & FISCH-MULLER S., 2007. - The genera of the Neotropical armored catfish subfamily Loricariinae (Siluriformes: Loricariidae): a practical key and synopsis. *Zootaxa*, 1462: 1-40.
- COVAIN R., LE BAIL P.-Y., SAGNES P. & FISCH-MULLER S., 2006. - Les espèces du genre *Harttia* (Siluriformes : Loricariidae) en Guyane française : morphologie, taxinomie et distribution. *Cybiu*, 30: 3-18.
- COVAIN R., DRAY S., FISCH-MULLER S. & MONTTOYA-BURGOS J.I., 2008. - Assessing phylogenetic dependence of morphological traits using co-inertia prior to investigate character evolution in Loricariinae catfishes. *Mol. Phylogenet. Evol.*, 46: 986-1002.
- COVAIN R., FISCH-MULLER S., MONTTOYA-BURGOS J.I., MOL J., LE BAIL P.Y. & DRAY S., 2009a. - Les Harttiini (Siluriformes, Loricariidae) des Guyanes : phylogénie et évolution des formes ou variation sur un même thème. In: Quatrièmes Rencontres de l'Ichtyologie en France, p. 40. Paris: SFI, IRD.
- COVAIN R., FISCH-MULLER S., MONTTOYA-BURGOS J.I., MOL J., LE BAIL P.Y. & DRAY S., 2009b. - Phylogeny and evolution of shapes: a new approach to predict phylogenetic positions of missing taxa. In: Sixième Symposium national de Morphométrie et Evolution des Formes, p. 41. GRD 2474 CNRS "Morphométrie et Evolution des Formes", Montpellier.
- COVAIN R., FISCH-MULLER S., MONTTOYA-BURGOS J.I., MOL J., LE BAIL P.Y. & DRAY S., 2009c. - Extracting phylogenetic signal in morphometric data to complete molecular phylogenies: a case study on Harttiini (Siluriformes, Loricariidae) from the Guianas. In: Thirteenth Evolutionary Biology Meeting at Marseilles, p. 80. Marseille: AEEB.
- DODSON P., 1978. - On the use of ratios in growth studies. *Syst. Zool.*, 27: 62-67.
- DRAY S. & DUFOUR A.B., 2007. - The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Soft.*, 22(4): 1-20.
- DRAY S., PETTORELLI N. & CHESEL D., 2003. - Multivariate analysis of incomplete mapped data. *Trans. GIS*, 7:411-422.
- EFRON B., 1979. - Bootstrap methods: another look at the jack-knife. *Ann. Stat.*, 7: 1-26.
- EIGENMANN C.H., 1912. - The freshwater fishes of British Guiana, including a study of the ecological grouping of species and the relation of the fauna of the plateau to that of the lowland. *Mem. Carneg. Mus.*, 5: 1-578, 103 pls.



- EVERS H.G. & SEIDEL I., 2005. - Catfish Atlas Vol. 1: South American Catfishes of the Families Loricariidae, Cetopsidae, Nematogenyidae and Trichomycteridae. 943 p. Melle: Mergus Verlag GmbH.
- FELSENSTEIN J., 1985. - Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39: 783-791.
- FERRARIS Jr C.J., 2003. - Subfamily Loricariinae (Armored catfishes). In: Check List of the Freshwater Fishes of South and Central America (CLOFFSCA) (Reis R.E., Kullander S.O. & Ferraris C. J., eds), pp. 330-350. Porto Alegre: EDIPUCRS.
- FERRARIS Jr C.J., 2007. - Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. *Zootaxa*, 1418: 1-628.
- FRICKE R. & ESCHMEYER W.N., 2010. - A guide to Fish Collections in the Catalog of Fishes database. On-line version of 15 Jan. 2010. <http://research.calacademy.org/redirect?url=http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>.
- GOWER J.C., 1966. - Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, 53: 325-338.
- GÜNTHER A., 1868. - Diagnoses of some new freshwater fishes from Surinam and Brazil, in the collection of the British Museum. *Ann. Mag. Nat. Hist.*, ser. 4, 1: 475-481.
- HALL T.A., 1999. - BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser.*, 41: 95-98.
- HEBERT P.D.N., CYWINSKA A., BALL S.L. & DE WAARD J.R., 2003. - Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. B.*, 270: 313-322.
- HEBERT P.D.N., STOECKLE M.Y., ZEMLAK T.S. & FRANCIS C.M., 2004. - Identification of birds through DNA barcodes. *PLoS Biol.*, 2:1657-1663.
- HILLS M., 1978. - On ratios - A response to Atchley, Gaskins, and Anderson. *Syst. Zool.*, 27: 61-62.
- HOLM S., 1979. - A simple sequentially rejective multiple test procedure. *Scand. J. Stat.*, 6: 65-70.
- HOREAU V., CERDAN P., CHAMPEAU A. & RICHARD S., 1998. - Importance of aquatic invertebrates in the diet of rapids-dwelling fish in the Sinnamary River, French Guiana. *J. Trop. Ecol.*, 14: 851-864.
- HUBERT N., HANNER R., HOLM E., MANDRAK N.E., TAYLOR E., BURRIDGE M., WATKINSON D., DUMONT P., CURRY A., BENTZEN P., ZHANG J., APRIL J. & BERNATCHEZ L., 2008. - Identifying Canadian freshwater fishes through DNA barcodes. *Plos One*, 3(6): e2490. Doi:10.1371/journal.pone.0002490.
- ISBRÜCKER I.J.H., 1973. - Redescription and figures of the South American mailed catfish *Rineloricaria lanceolata* (Günther, 1868) (Pisces, Siluriformes, Loricariidae). *Beaufortia*, 278: 75-89.
- ISBRÜCKER I.J.H., 1979. - Descriptions préliminaires de nouveaux taxa de la famille des Loricariidae, poissons-chats cuirassés néotropicaux, avec un catalogue critique de la sous-famille nominale (Pisces, Siluriformes). *Rev. Fr. Aquariol.*, 5: 86-116.
- ISBRÜCKER I.J.H., 1980. - Classification and catalogue of the mailed Loricariidae (Pisces, Siluriformes). *Versl. Tec. Geg., Inst. Taxon. Zool. (Zool. Mus.)*, 22: 1-181.
- ISBRÜCKER I.J.H., 2001. - Nomenklator der Gattungen und Arten der Harnischwelse, Familie Loricariidae Rafinesque, 1815 (Teleostei, Ostariophysi). *Datz Harnischwelse*, 2: 25-32.
- ISBRÜCKER I.J.H., 2002. - Nomenclator of the 108 genera with 692 species of the mailed catfishes, family Loricariidae Rafinesque, 1815 (Teleostei, Ostariophysi). *Cat Chat, J. Catfish Stud. Group (UK)*, 3: 11-30.
- ISBRÜCKER I.J.H., SEIDEL I., MICHELS J.P., SCHRAMLE E. & WERNER A., 2001. - Diagnose vierzehn neuer Gattungen der Familie Loricariidae Rafinesque, 1815 (Teleostei, Ostariophysi). In: Harnischwelse 2 (Stawikowski R., ed.), pp. 17-24. Stuttgart, Germany: Die Aquarien und Terrarien Zeitschrift, Sonderheft, Eugen Ulmer.
- JOMBART T., MOAZAMI, GOUDARZI K., DUFOUR A.B. & LALOË D., 2006. - Fréquences alléliques et cohérence entre marqueurs moléculaires : des outils descriptifs. *Actes BRG*, 6: 25-39.
- JOMBART T., BALLOUX F. & DRAY S., 2010. - Adephylo: new tools for investigating the phylogenetic signal in biological traits. *Bioinformatics*, 26: 1907-1909.
- KEITT T., 2009. - ColorRamps: builds color tables. R package version 2.3. <http://CRAN.R-project.org/package=colorRamps>.
- KIMURA M., 1980. - A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.*, 15: 111-120.
- LANGEANI F., OYAKAWA O.T. & MONTOYA-BURGOS J.I., 2001. - New species of *Harttia* (Loricariidae, Loricariinae) from the São Francisco Basin. *Copeia*, 2001: 136-142.
- LE BAIL P.Y., KEITH P. & PLANQUETTE P., 2000. - Atlas des Poissons d'eau douce de Guyane. Tome 2, fascicule II: Siluriformes. 307 p. *Patrimoines Nat.*, 43(2). Paris: MNHN/SPN.
- LEGENDRE P. & LAPOINTE F.J., 2004. - Assessing congruence among distance matrices: single malt Scotch whiskies revisited. *Aust. N.Z. J. Stat.*, 46: 615-629.
- LÉVÊQUE C., OBERDORFF T., PAUGY D., STIASNY M.L.J. & TEDESCO P.A., 2008. - Global diversity of fish (Pisces) in freshwater. *Hydrobiologia*, 595: 547-567.
- MANTEL N., 1967. - The detection of disease clustering and a generalized regression approach. *Cancer Res.*, 27: 209-220.
- MÉRONA B. de, 2005. - Le Fleuve, le Barrage et les Poissons. Le Sinnamary et le Barrage de Petit-Saut en Guyane française. 135 p. Paris: Editions IRD.
- MEYER C.P. & PAULAY G., 2005. - DNA barcoding: error rates based on comprehensive sampling. *PLoS Biol.*, 3: 2229-2238.
- MOL J.H. & OUBOTER P.E., 2004. - Downstream effects of erosion from small-scale gold mining on the instream habitat and fish community of a small neotropical rainforest stream. *Conserv. Biol.*, 18: 201-214.
- MOL J.H., WAN TONG YOU K., VREDE I., FLYNN A., OUBOTER P. & VAN DER LUGT F., 2007. - Fishes of Lely and Nassau Mountains, Suriname. In: A Rapid Biological Assessment of the Lely and Nassau Plateau, Suriname (with additional information on the Brownsberg Plateau) (Alonso L.E. & J.H. Mol, eds), pp. 107-118. RAP Bulletin of Biological Assessment 43. Arlington, USA: Conservation International.
- MONTOYA-BURGOS J.I., MULLER S., WEBER C. & PAWLOWSKI J., 1998. - Phylogenetic relationships of the Loricariidae (Siluriformes) based on mitochondrial rRNA gene sequences. In: Phylogeny and Classification of Neotropical Fishes (Malabarba L.R., Reis R.E., Vari R.P., Lucena Z.M.S. & Lucena C.A.S., eds), pp. 363-374. Porto Alegre: EDIPUCRS.

- MORAN P.A.P., 1950. - Notes on continuous stochastic phenomena. *Biometrika*, 37: 17-23.
- NÉGREL P. & LACHASSAGNE P., 2000. - Geochemistry of the Maroni River (French Guiana) during the low water stage: implications for water-rock interaction and groundwater characteristics. *J. Hydrol.*, 237: 212-233.
- PARADIS E., 2006. - Analysis of Phylogenetics and Evolution with R. 211 p. New York: Springer.
- PARADIS E., CLAUDE J. & STRIMMER K., 2004. - APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20: 289-290.
- PAVOINE S., OLLIER S., PONTIER D. & CHESSEL D., 2008. - Testing for phylogenetic signal in life history variable: Abouheif's test revisited. *Theor. Popul. Biol.*, 73: 79-91.
- PLANQUETTE P., KEITH P. & LE BAIL P.Y., 1996. - Atlas des Poissons d'eau douce de Guyane. Tome 1. 429 p. Collection Patrimoine Nat., 22. Paris: IEGB-MNH, INRA, CSP, Min. Environ.
- PROVENZANO R.F., MACHADO-ALLISON A., CHERNOFF B., WILLINK P. & PETRY P., 2005. - *Harttia merevari*, a new species of catfish (Siluriformes: Loricariidae) from Venezuela. *Neotrop. Ichthyol.*, 3: 519-524.
- R DEVELOPMENT CORE TEAM, 2009. - R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- RAPP PY-DANIEL L.H. & OLIVEIRA E.C., 2001. - Seven new species of *Harttia* from the Amazonian-Guyana region (Siluriformes: Loricariidae). *Ichthyol. Explor. Freshw.*, 12: 79-96.
- REGAN C.T., 1904. - A monograph of the fishes of the family Loricariidae. *Trans. Zool. Soc. Lond.*, 17: 191-350, pls 199-121.
- SAITOU N. & NEI M., 1987. - The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.*, 4: 406-425.
- SARKAR D., 2010. - Lattice: lattice graphics. R package version 0.18-3. <http://CRAN.R-project.org/package=lattice>.
- SONDAG F., GUYOT J.L., MOQUET J.S., LARAQUE A., ADÈLE G., COCHONNEAU G., DOUDOU J.C., LAGANE C. & VAUCHEL P., 2010. - Suspended sediment and dissolved load budgets for two Amazonian rivers of French Guiana: Maroni and Oyapock rivers. *Hydrol. Process.*, 24: 1433-1445.
- TENENHAUS M., 1998. - La Régression PLS: Théorie et Pratique. 254 p. Paris: Editions Technip.
- THIOULOUSE J. & DRAY S., 2007. - Interactive multivariate data analysis in R with the ade4 and ade4TkGUI packages. *J. Stat. Soft.*, 22(5): 1-14.
- VALDEZ-MORENO M., IVANOVA N.V., ELÍAS-GUTIÉRREZ M., CONTRERAS-BALDERAS S. & HEBERT P.D.N., 2009. - Probing diversity in freshwater fishes from Mexico and Guatemala with DNA barcodes. *J. Fish Biol.*, 74: 377-402.
- VARI R.P. & FERRARIS JR C.J., 2009. - Fishes of the Guiana Shield. In: Checklist of the Freshwater Fishes of the Guiana Shield (Vari R.P., Ferraris Jr C.J., Radosavljevic A. & Funk V.A., eds). *Bull. Biol. Soc. Washington*, 17: 9-18.
- VARI R.P., FERRARIS JR C.J., RADOSAVLJEVIC A. & FUNK V.A., 2009. - Checklist of the Freshwater Fishes of the Guiana Shield. *Bull. Biol. Soc. Wash.*, no. 17: i-vii, 1-95.
- WARD R.D., 2009. - DNA barcode divergence among species and genera of birds and fishes. *Mol. Ecol. Res.*, 9: 1077-1085.
- WARD R.D., WOODWARK M. & SKININSKI D.O.F., 1994. - A comparison of genetic diversity levels in marine, freshwater and anadromous fish. *J. Fish Biol.*, 44: 213-232.
- WARD R.D., ZEMLAK T.S., INNES B.H., LAST P.R. & HEBERT P.D.N., 2005. - Barcoding Australia's fish species. *Phil. Trans. R. Soc. B*, 360: 1847-1857.
- WARD R.D., HANNER R. & HEBERT P.D.N., 2009. - Review paper: the campaign to DNA barcode all fishes, FISH-BOL. *J. Fish Biol.*, 74: 329-356.
- WATSON D.J. & BALON E.K., 1984. - Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. *J. Fish Biol.*, 25: 371-384.
- WOLD H., 1966. - Estimation of principal components and related models by iterative least squares. In: Multivariate Analysis (Krishnaiah P., ed.), pp. 391-420. New York: Academic Press.
- XIA X. & XIE Z., 2001. - DAMBE: Data analysis in molecular biology and evolution. *J. Hered.*, 92: 371-373.
- XIA X., XIE Z., SALEMI M., CHEN L. & WANG Y., 2003. - An index of substitution saturation and its application. *Mol. Phylogenet. Evol.*, 26: 1-7.

### List of supporting files

Available on Cybium website: <http://www.mnhn.fr/sfi/cybium/cybium/numeros/361/sommaire361.html>

- S1. - *Cteniloricaria platystoma*, MHNG 2704.016, 171.78 mm SL, Suriname, Sipaliwini River, Paikali rapid.
- S2. - *Cteniloricaria platystoma* in life for different populations. **A**: Guyana, Essequibo River, Kurupukari Cross (R. Covain); **B**: Suriname, Corantijn River, Cow Falls (R. Covain); **C**: Suriname, Suriname River, Assigon (R. Covain); **D**: Suriname, Paloemeu River, Weyu Camp (R. Covain).
- S3. - *Harttiella crassicauda*, MHNG 2674.051 (specimen MUS 221), 38.00 mm SL, Suriname, Nassau Mountains, Paramaka Creek.
- S4. - *Harttiella* spp. in life. **A**: *H. crassicauda*, Suriname, Nassau Mountains, Paramaka Creek (T. Larsen); **B**: *H. pilosa*, French Guiana, Tortue Mountains, Orapu River drainage in Crique Grillon (R. Covain).
- S5. - *Harttia guianensis*, MHNG 2643.008, 146.07 mm SL, French Guiana, Litani River, vicinity of Antecume Pata.
- S6. - *Harttia* spp. in life. **A**: *H. guianensis*, Suriname, Paloemeu River, Weyu Camp (R. Covain); **B**: *H. surinamensis*, Suriname, Suriname River, Gran Rio (R. Covain); **C**: *H. fowleri*, French Guiana, Oyapock River, Alikoto Falls (R. Covain); **D**: *H. fowleri*, French Guiana, Oyapock River, Moulou Koulou (R. Covain).
- S7. - *Harttia surinamensis*, MHNG 2673.033 (specimen SU05-230), 183.98 mm SL, Suriname, Suriname River, Cajana Creek.
- S8. - *Harttia fowleri*, MHNG 2680.091 (specimen GF06-016), 210.47 mm SL, French Guiana, Oyapock River, Alikoto Falls.